

Record breeding densities of Frances's Sparrowhawk *Accipiter francesiae*, and effects on bird communities in the Comoros

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ABSTRACT. - In two study plots on Mayotte Island, the territorial, neotenic-endemic race *brutus* of the Frances's Sparrowhawk occurred at world-record breeding densities for a small raptor of 2.0-2.6 ha/pair, with average inter-nest distances of 140-159 m in the breeding season of 1997. Measured in nine transects, the abundance of birds of potential prey-size correlated negatively with sparrowhawk abundance on Mayotte, while numbers of birds larger than sparrowhawks varied in parallel with sparrowhawk abundance, both corresponding to rainfall and lushness of the vegetation. Throughout the Comoro archipelago, there is a negative relationship at island level between sparrowhawk abundance and the proportion of small birds in the community. Several species of small birds are lacking from islands with sparrowhawks compared to islands without sparrowhawks; anomalies that cannot be explained by island size, distance to source or habitat. More species are lacking from islands with high sparrowhawk abundance. We suspect that the chances of survival for colonizing birds may have been affected historically by the abundance of Frances's Sparrowhawks on some of the Comoro Islands.

Introduction

Several Falconiforms breed colonially, and many other raptors form loose breeding associations with high densities of nests under exceptional conditions of food abundance (Cramp and Simmons 1980, del Hoyo *et al.* 1994). Although the immediate vicinity of the nest is usually defended against conspecifics also under colonial conditions, hunting grounds are communal. Truly territorial raptors, i.e. species which obtain most of their requirements from within the boundaries of an exclusive territory which is defended against intrusions by conspecifics other than the breeding mate or offspring, have their nests regularly spaced at intervals which reflect the space requirements of the species in relation to the quality of the habitat (Newton 1979, 1986, Marquiss and Newton 1982, Newton *et al.* 1986): e.g. densities on the European continent are 2-62 pairs/100 km² in the small, territorial Eurasian Sparrowhawk *Accipiter nisus* (Forsman and Solonen 1984, Newton 1986, Blondel *et al.* 1988, Bühler 1991, Bijlsma 1993, Tomialojc and Wesolowski 1996), while densities are slightly higher 14-96 pairs/100 km² in Great Britain, where inter-nest distances are typically 0.5-2.1 km (Newton *et al.* 1986, Newton 1986). In the genus *Accipiter*, territorial raptors, particularly "high densities" are reported from such islands as Taveuni (Fiji) (Clunie 1981), New Caledonia (Thiollay 1993) and (particular) Solomon islands (Webb 1997).

Indeed, animal densities are in general higher on islands than on the adjacent mainland (MacArthur *et al.* 1972, Williamson 1981, Crowell 1983, Blondel 1986),

which has sometimes been ascribed to lower levels of predation (Faeth 1984, George 1987). The principle of density inflation on islands does also hold for raptors (Thibault *et al.* 1992, Thiollay 1993, Pérez del Val *et al.* 1994), and consequently, adjacent islands which have or lack a raptor species can be subject to very different levels of predation.

Frances's Sparrowhawk *Accipiter francesiae* is a small sparrowhawk (males 100 g, females 150 g: Herremans *et al.* 2001) endemic to the Malagasy region (del Hoyo *et al.* 1994), with distinct subspecies on Madagascar and on each of three Comoro Islands, while it is absent from the fourth island, Moheli (Mwali). Sexes on Madagascar have well differentiated plumages, but on each Comoro island, sexes are similar. In the race *brutus* on Mayotte (Maore), birds have brown upperparts and are heavily barred brown underneath, closely resembling the female and juvenile plumage from Madagascar; on Grand Comoro (Ngazidja) and Anjouan (Ndzuani), both sexes have a masculine plumage (Benson 1960, Louette 1988, Langrand 1990, Louette 2000). Compared to the nominate form in Madagascar, *brutus* on Mayotte is partially neotenic (Herremans 1990). A relationship between neotenic evolution, e.g. in plumages and reduced territoriality (Herremans 1990), and increased densities has been shown on the Comoros as one of the 'insular syndromes' shared by several species (Louette *et al.* 1993a). From point-transect counts of birds in October 1992 (Louette *et al.* 1993b), 1993 and 1994 (Stevens and Louette 1999), we became aware that this sparrowhawk is particularly abundant on Mayotte. We observed several successful attempts to prey on reptiles, and we witnessed that the sparrowhawk readily responds to traps baited with small birds. Mizuta (2007) mentions the direct observation of predation of this sparrowhawk on a small bird.

Predator populations typically follow prey dynamics (e.g. Newton 1991), but experimental predator control did only in about half the studies result in an increase of prey populations, indicating that other factors than predation were limiting (Newton 1991). All cases where predator removal resulted in an increase of bird breeding populations refer to vulnerable ground nesting species which were secondary or alternative prey for predators with population levels supported by a staple food (other than birds) that failed occasionally or cyclic (Newton 1991). During the comprehensive studies of the Eurasian Sparrowhawk, a systematic effects of the predator on the population sizes of a prey species, the House Sparrow *Passer domesticus*, was detected in Britain (Bell *et al.* 2010), and also an impact on Grey Partridge *Perdix perdix*, where the prey numbers were at low levels (Park *et al.* 2008). Sometimes severe temporal or local impact on some species or age categories was found (Newton 1986, Whitfield *et al.* 1988, Newton *et al.* 1997). Frances's Sparrowhawks are the only important avian predator on small forest birds in the Comoros: numbers of Peregrine Falcon *Falco peregrinus*, Sooty Falcon *F. concolor*, Eleonora's Falcon *F. eleonorae*, and Yellow-billed Kite *Milvus parasitus* are small, and the first species preys mainly on waders, the second and third on insects and the fourth is not specialized on birds; Madagascar Harrier *Circus maillardi*, which is nowadays absent from Mayotte feeds largely on rodents (Benson 1960, Louette 1988). Barn Owl *Tyto alba* occasionally preys on birds, but its staple food on Mayotte is the Black Rat *Rattus rattus*, itself a nest predator of small birds (Louette 1996b, 1998).

The present paper reports world-record breeding densities for a sparrowhawk

from the Comoros, and investigates whether and how these might have affected the bird communities on the islands.

Material and Methods

Densities. — During bird studies on the Comoros (1981-2001), we kept annotated daily lists of species observed. From these lists, we calculated the daily reporting rate of sparrowhawks (fraction of lists in which sparrowhawks were seen) to compare abundance on Grand Comoro and Anjouan. During nine point-transect counts on Mayotte in October 1993, the distance between bird and observer was estimated. This enabled the calculation of densities in concentric bands around the observer (Bibby *et al.* 1992).

In August 1995, at the onset of the breeding season, Frances's Sparrowhawks were inventoried in the western quarter of the Coconi study-plot (Fig. 1A) by a method called "trefclus" in use for passerines occurring at high density (Bult 1995). After familiarization, each morning from 27 August till 1 September between 7-8h two observers (M. Louette and an assistant) walked in opposite directions along a 2.25 km path. All sparrowhawk contacts were plotted on a map. This yielded a 6-day position map of (supposed) individuals. This procedure was repeated during 5 days in August 1996.

Breeding densities. — We studied breeding densities of Frances's Sparrowhawks at two sites in the wet western sector of Mayotte between 13 December 1997 and 14 January 1998: (A) 75 ha of small-scale plantations and crop farming with remnants of indigenous forest, accessible via a multitude of tracks, situated immediately NE of the Coconi forestry station; this site encompassed the study site of 1995 and 1996 (Fig. 1A); (B) 61 ha 10 km further north, between the villages of Tsingoni and Mrowalé. This was less accessible and we made inventories from tracks along two small river valleys, and in a coconut plantation on the adjacent plateau; a central part of this site was too far from the tracks and is excluded (Fig. 1B). We visited the study area at Coconi during 65 hours on 21 days, and Mrowalé during 29 hours on 8 days.

While walking study plots slowly, M. Herremans called up Frances's Sparrowhawks by imitating the territorial call ("vhit vhit vhit"), or the higher pitched and huskier begging call of juveniles ("whiest whiest whiest"). Dependent on topography, birds could be heard up to 100 m away, and where response was received, we searched the area systematically for the nest. Nests were plotted on a detailed map, and once a pattern of regular spacing of nests emerged, gaps were particularly carefully searched for nests or presence of territorial birds. Where nests had not yet been found, we watched adults for signs of breeding behavior. Where territorial boundaries were not resolved, we released caught and ringed sparrowhawks 100-200 m from the place of capture, to provoke response from neighboring territories. We also used resightings of ringed birds to differentiate territories. We recorded nest positions with an MX8600-pc GPS and GPS-Leica 2.40 groundstation software, resulting in an accuracy of <5 m. Boundaries of the study areas were determined in a GIS environment, using distance from the inventory tracks and topography as the main features.

Bird communities. — We sampled bird communities (mostly in forests) on the Comoros during 1985-1995 by point-transect counts. Each transect consisted of 20 points, where birds were counted for 15 minutes. We only use in this study counts from the breeding season (October-December). We used 31 transect counts from Grand Comoro, of which eight were repeats in two different years (Louette *et al.* 1988a, Stevens *et al.* 1995). We counted three transects on Moheli (Louette *et al.* 1989). We repeated nine transects during three years on Mayotte (Louette *et al.* 1993b, Stevens and Louette 1999). Repeated counts were averaged. We use the number of birds observed in transects as a measure of relative abundance. Assuming that abundance of a species was similar for repeated counts, detectability of the species can be deduced from the year to year variation; we define detectability as the fraction of the minimum to the maximum count in a transect.

Based on our own data on body mass of Comoro birds, we allocated species to weight classes: (1) likely prey <20g, (2) possible prey 20-<70g, (3) 70-<150g, (4) ≥150g. We consider categories (1) and (2) as ‘potential prey’, while (3) and (4) are no regular prey of Frances’s sparrowhawks (although Clément *et al.* 2008 show a picture of a Frances’ Sparrowhawk grabbing such an unlikely prey as a Dabchick *Tachybaptus ruficollis*). We excluded aerial foragers that are not directly part of the forest bird-community interacting with sparrowhawks (e.g. the Black Swift *Apus barbatus*) from these analyses. However, the Spinetail Swift *Zoonavena grandidieri*, which forages extensively below the canopy and might be taken by sparrowhawks, was included.

The forest patch on La Grille, the northern volcano on Grand Comoro is isolated by inhospitable recent lava flows from the Karthala, the southern volcano. La Grille lacks several bird species present on the Karthala (Louette *et al.* 2008). For inter-island comparisons, La Grille is given the status of a separate ‘zoogeographical island’. On Anjouan, Moheli and Mayotte, forest species occur down to sea level, but on Grand Comoro there is a dry coastal zone where habitat for forest species is lacking (except on the wettest southwestern flank of the Karthala). We include only estimated surfaces of potential habitat, and exclude for Grand Comoro the dry coastal zone, the large areas of inhospitable recent lava fields and the montane zone (absent on the other islands). To compare forest species numbers between islands, the following areas were used to compensate for island size: Moheli=250 km², Mayotte=374 km², Anjouan=425 km², Grand Comoro (Karthala)=450 km², Grand Comoro (Grille)=225 km².

Results

Density. — Except for their conspicuous behavior near nests and responsiveness to calls, Frances’ Sparrowhawks were unobtrusive and remarkably infrequently encountered on Mayotte. Our data demonstrate this as follows: (1) variability of numbers encountered in transect counts was high, with a mean detectability of 0.36 (range 0.13-0.64), Frances’s Sparrowhawk was the second least stable species (after Madagascar Turtle Dove *Streptopelia picturata*); (2) while undoubtedly the same number of birds is present during counts in the morning and in the afternoon, 45% fewer were detected in the afternoon ($X^2_{df=1}=34.8, P<0.00001$); (3) during the standardized census work in

August 1995 and 1996 at Coconi, the average number of encounters with sparrowhawks during an hour in the morning varied between 0-15 birds (average 5.6), while ‘trefclus’ and subsequent data on the number of nests normally present in this area indicate that in fact there were about 12-14 adults and possibly some unpaired floaters present; (4) during the 6-day census at Coconi in August 1995, the probability to detect one member of a pair in a single morning was 52% (assuming seven pairs and no floaters in part of the Coconi plot).

Daily reporting rates in the years 1983 - 1992 were 0.2 on Anjouan (sparrowhawks seen on three days out of 14) and 0.3 on the Karthala (16 days out of 49). In 2005, the reporting rate on Anjouan was higher: 0.47 – seven days out of 15 - C. Marsh in Louette *et al.* 2008). Density estimates on concentric bands from point-transect counts indicated a rapidly declining detectability of sparrowhawks beyond 50 m, and an average density of >1 bird/ha throughout the densely vegetated wet sector of Mayotte in October 1993 (Table 1).

Non-nesting adults were difficult to inventory, and immature floaters were observed only on three occasions during 1997-98. Several factors greatly facilitated the inventarisation of Frances’s Sparrowhawk nests on Mayotte during December-January: details on the synchronization and phenology of breeding, the exposed nest positions, the conspicuous behavior around the nest and the extreme tameness are reported elsewhere (Herremans *et al.* 2001). With the full inventory at hand, with hindsight, 70% of females called back within minutes in response to imitations and were discovered in the first visit, while during a single visit of a few minutes, on average 63% of known sites were re-confirmed by calling young when less than one month fledged.

In the study plot at Coconi, we found 29 pairs in an area of 75 ha; 20 pairs fledged young, two were still incubating by the end of the study in January 1998 and seven failed, in four of which the empty nest was found. No evidence of breeding could be found for three pairs (Fig. 1A). At Mrowalé, we found 30 pairs in 61 ha; 19 fledged young, eight nests failed and for three pairs no evidence of breeding could be found (Fig. 1B). We investigated particularly the nests closest to each other for signs of polygyny by catching the adults, but no cases of polygyny were recorded.

Table 1. Density estimates of Frances’s Sparrowhawk *Accipiter francesiae brutus* in concentric zones (Bibby *et al.* 1992) around 180 points in transect-counts on Mayotte in October 1993 (unpubl. data JS).

Radius of zone (m)	Number of sparrowhawks observed	Density (birds/ha)
<25	45	1.27
25-<50	93	0.98
50-<75	15	0.48
75-<100	28	0.32
100-150	24	0.16

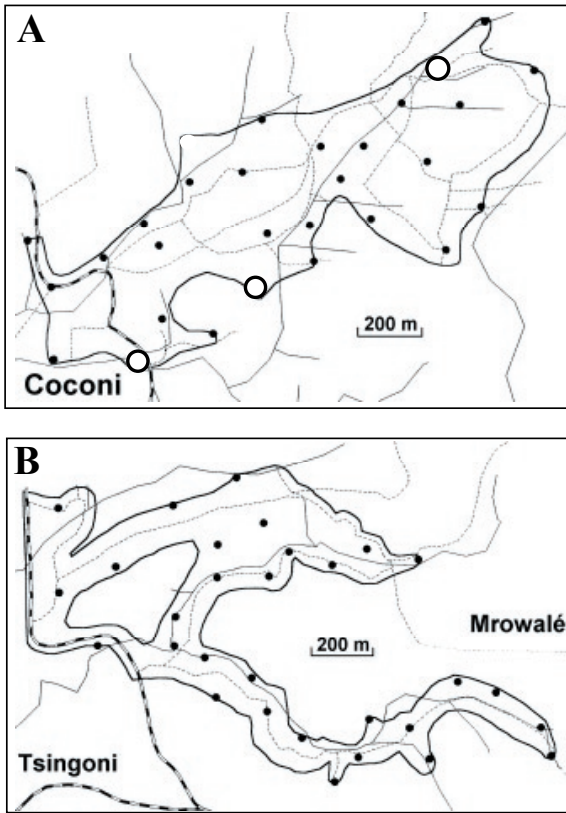


Figure 1. Spacing of Frances's Sparrowhawk *Accipiter francesiae brutus* nests and territories at two study sites on Mayotte (Comoro Islands) during December 1997-January 1998: 1A. Coconi; 1B. Mrowalé.

Average nearest-neighbor distances between nests (or territory centers) were 158.5 m (SE 7.0, range 87-234 m, $n=29$) at Coconi and 140.2 m (SE 7.9, range 101-274 m) at Mrowalé (Fig. 2). Second-nearest neighbor analyses showed that 63% of all occupied nests were within 200 m of two other occupied nests.

Sparrowhawks and bird communities on Mayotte. — The numbers of small, 'likely prey' birds (<20g) correlated negatively with sparrowhawk abundance on Mayotte, while those of birds in the category 20-70g showed a weak similar tendency (Fig. 3). In contrast, numbers of 'larger' birds (>70g) other than sparrowhawks were higher in places with more sparrowhawks (Fig. 3); the difference between both trendlines of potential prey and non-prey species is significant ($P<0.01$; $P<0.05$). There was also a significant negative trend on Mayotte between the number of sparrowhawks recorded in transects and the proportion of potential prey species in the overall number of birds other than sparrowhawks ($rs=-0.62$, $P<0.05$; Fig. 4 inset).

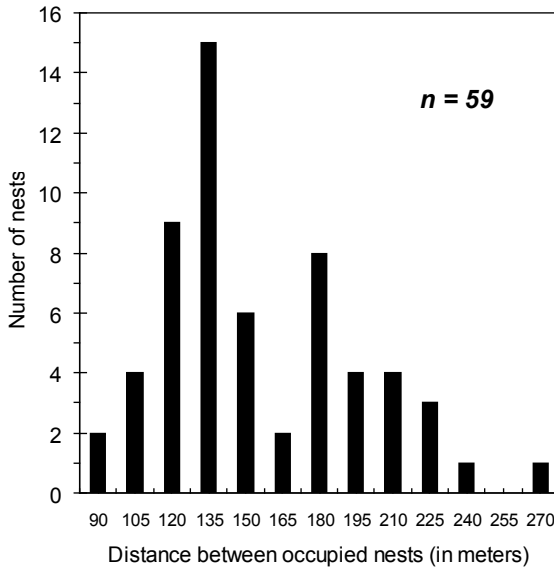


Figure 2. Nearest-neighbor distances of Frances's Sparrowhawk *Accipiter francesiae brutus* nests and territory centers on Mayotte Island.

In a stepwise multiple regression, sparrowhawk numbers were not significantly explained by a model containing only 'environmental' variables (rainfall, altitude and seven vegetation parameters), though rainfall (positive) and altitude (negative) accounted for 52% of the variation in sparrowhawk numbers (Table 2). Potential prey species had 47% of variation in numbers explained by altitude (negative) and a further 9% by rainfall (negative). When bird numbers were included in the regressions, they became significant. Sparrowhawk numbers varied in parallel to the variation in numbers of other larger birds (excluding sparrowhawks), and correlated with parameters of more lush vegetation (Table 2); abundance of potential prey species did not contribute to this model. On the other hand, sparrowhawk numbers alone explained 33% of the variation in the abundance of potential prey species (negative correlation) (Table 2). Small birds were furthermore concentrated at lower altitude and in lower vegetation (Table 2).

Sparrowhawks and Comoro bird faunas — The Comoro bird fauna's show a number of anomalies: some abundant, widespread and good colonizing species are inexplicably absent from some islands. We constructed a presence/absence table for not introduced, terrestrial species to investigate whether there would be a predictable sequence of species loss merely related to island size. If the relation was purely and predictably island-size related, we would expect only 0's in the top left of Table 3, and only 1's in the right bottom corner (Simberloff and Levin 1985). Any deviation from that pattern needs permutations of the data to obtain a sequence with exclusively 0's followed by

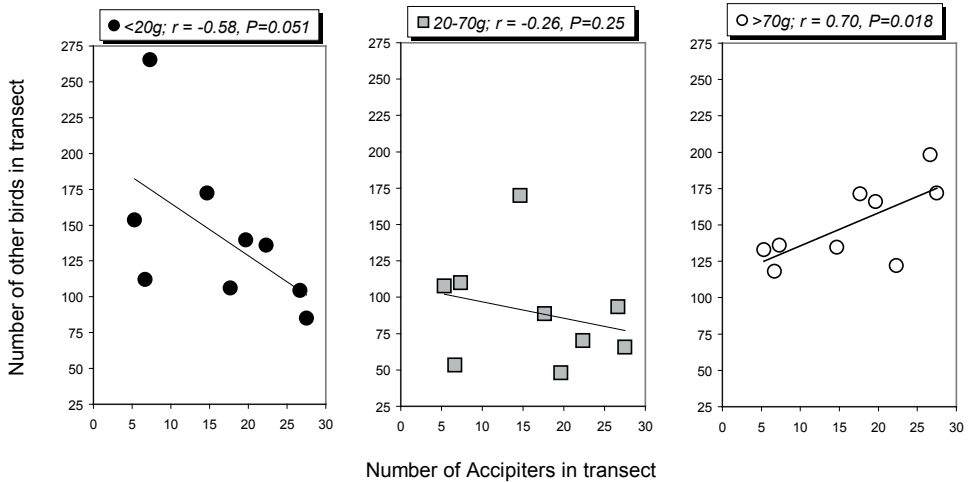


Figure 3. Relationship between Frances's Sparrowhawk *Accipiter francesiae brutus* numbers and numbers of other birds in the weight categories of likely prey (<20g), possible prey (20-70g) and no prey (>70g) in transect-counts on Mayotte Island.

Table 2. Main factors in stepwise multiple regressions on bird community and environmental variables on Mayotte Island.

VARIABLES					
Dependent	Step	Independent	Significant	Contribution to R ²	Significance
<u>Models including only environmental variables:</u>					
Accipiters	1	Rainfall (+)	no	27%	<i>P</i> = 0.15
	2	Altitude (-)	no	25%	
	3	% shrubs (+)	no	15%	
Potential prey	1	Altitude (-)	no	47%	<i>P</i> = 0.08
	2	Rainfall (-)	no	9%	
<u>Models including environmental and bird population variables:</u>					
Accipiters	1	Larger birds (+)	yes	46%	<i>P</i> = 0.002
	2	% shrubs (-)	yes	10%	
	3	% bare ground (-)	yes	24%	
	4	% small trees (+)	yes	10%	
	5	% dead trees (-)	yes	8%	
Potential prey	1	Altitude (-)	no	47%	<i>P</i> = 0.026
	2	Accipiters (-)	yes	33%	
	3	Vegetation height (-)	yes	9%	
	4	% dead trees (+)	no	3%	
	5	% bare ground (-)	no	4%	

Table 3. Presence/absence table of landbirds breeding on the Comoros as a function of island size; birds in order of increasing number of islands occupied and increasing number of permutations needed, islands in order of increasing size. Permutations are the number of steps necessary to convert the observed sequence for a species to one fitting the ‘island-size model’ whereby a series of absences (0) on the smaller islands is followed by a series of presence (1) on the larger islands. LG - La Grille, Mh - Moheli, My - Mayotte, A - Anjouan, K - Karthala, Is - number of islands occupied P - permutations, W - weight class

Area (km ²)	LG 225	Mh 250	My 374	A 425	K 450	Is	P	W
<u>Endemic taxa</u>								
<i>Accipiter francesiae griveaudi</i>	0	0	0	0	1	1	0	3
<i>Otus pauliani</i>	0	0	0	0	1	1	0	3
<i>Leptosomus discolor gracilis</i>	0	0	0	0	1	1	0	4
<i>Cyanolanius madagascarinus bensoni</i>	0	0	0	0	1	1	0	2
<i>Humblotia flaviviridis</i>	0	0	0	0	1	1	0	1
<i>Zosterops mouroniensis</i>	0	0	0	0	1	1	0	1
<i>Dicrurus fuscipennis</i>	0	0	0	0	1	1	0	3
<i>Accipiter francesiae pusillus</i>	0	0	0	1	0	1	1	3
<i>Otus capnodes</i>	0	0	0	1	0	1	1	3
<i>Leptosomus discolor intermedius</i>	0	0	0	1	0	1	1	4
<i>Turdus bewsheri bewsheri</i>	0	0	0	1	0	1	1	2
<i>Nesillas typica longicaudata</i>	0	0	0	1	0	1	1	1
<i>Terpsiphone mutata vulpina</i>	0	0	0	1	0	1	1	1
<i>Nectarinia souimanga comorensis</i>	0	0	0	1	0	1	1	1
<i>Zosterops maderaspatana anjouanensis</i>	0	0	0	1	0	1	1	1
<i>Foudia eminentissima anjouanensis</i>	0	0	0	1	0	1	1	2
<i>Dicrurus forficatus potior</i>	0	0	0	1	0	1	1	3
<i>Accipiter francesiae brutus</i>	0	0	1	0	0	1	2	3
<i>Otus rutilus mayottensis</i>	0	0	1	0	0	1	2	3
<i>Terpsiphone mutata pretiosa</i>	0	0	1	0	0	1	2	1
<i>Nectarinia coquereli</i>	0	0	1	0	0	1	2	1
<i>Zosterops maderaspatana mayottensis</i>	0	0	1	0	0	1	2	1
<i>Foudia eminentissima algondae</i>	0	0	1	0	0	1	2	2
<i>Dicrurus waldenii</i>	0	0	1	0	0	1	2	3
<i>Treron australis griveaudi</i>	0	1	0	0	0	1	3	4
<i>Otus moheliensis</i>	0	1	0	0	0	1	3	3
<i>Coracina cinerea moheliensis</i>	0	1	0	0	0	1	3	2
<i>Hypsipetes parvirostris moheliensis</i>	0	1	0	0	0	1	3	2
<i>Cyanolanius madagascarinus comorensis</i>	0	1	0	0	0	0	1	32
<i>Turdus bewsheri moheliensis</i>	0	1	0	0	0	1	3	2
<i>Nesillas mariae</i>	0	1	0	0	0	1	3	1
<i>Nesillas typica moheliensis</i>	0	1	0	0	0	1	3	1
<i>Terpsiphone mutata voeltzkowiana</i>	0	1	0	0	0	1	3	1
<i>Nectarinia humbloti mohelica</i>	0	1	0	0	0	1	3	1
<i>Nectarinia notata voeltzkowi</i>	0	1	0	0	0	1	3	1
<i>Foudia eminentissima eminentissima</i>	0	1	0	0	0	1	3	2
<i>Zosterops maderaspatana comorensis</i>	0	1	0	0	0	1	3	1
<i>Coracopsis nigra sibilans</i>	0	0	0	1	1	2	0	4

Table 3. continued

Area (km ²)	LG 225	Mh 250	My 374	A 425	K 450	Is	P	W
<i>Zoonavena grandidieri mariae</i>	1	0	0	0	1	2	3	1
<i>Coracina cinerea cucullata</i>	1	0	0	0	1	2	3	2
<i>Hypsipetes parvirostris parvirostris</i>	1	0	0	0	1	2	3	2
<i>Saxicola torquata voeltzkowi</i>	1	0	0	0	1	2	3	1
<i>Turdus bewsheri comorensis</i>	1	0	0	0	1	2	3	2
<i>Nesillas brevicaudata</i>	1	0	0	0	1	2	3	1
<i>Terpsiphone mutata comorensis</i>	1	0	0	0	1	2	3	1
<i>Zosterops maderaspatana kirki</i>	1	0	0	0	1	2	3	1
<i>Nectarinia humbloti humbloti</i>	1	0	0	0	1	2	3	1
<i>Nectarinia notata moebii</i>	1	0	0	0	1	2	3	1
<i>Foudia eminentissima consobrina</i>	1	0	0	0	1	2	3	2
<i>Coracopsis vasa comorensis</i>	1	1	0	1	1	4	2	4
<i>Columba polleni</i>	1	1	1	1	1	5	0	4
<i>Alectroenas sganzini</i>	1	1	1	1	1	5	0	4
<i>Cypsiurus parvus griveaudi</i>	1	1	1	1	1	5	0	1
<i>Apus barbatus mayottensis</i>	1	1	1	1	1	5	0	2
<i>Streptopelia picturata comorensis</i>	1	1	1	1	1	5	0	4
<u>Not endemic taxa</u>								
<i>Leptosomus discolor discolor</i>	0	1	1	0	0	2	4	4
<i>Circus maillardi macroscelus</i>	1	1	1	1	1	5	0	4
<i>Falco peregrinus radama/perconfusus</i>	1	1	1	1	1	5	0	4
<i>Coturnix coturnix erlangeri</i>	1	1	1	1	1	5	0	3
<i>Turtur tympanistria</i>	1	1	1	1	1	5	0	2
<i>Streptopelia capicola tropica</i>	1	1	1	1	1	5	0	3
<i>Tyto alba affinis</i>	1	1	1	1	1	5	0	4
<i>Agapornis cana cana</i>	1	1	1	1	1	5	0	2
<i>Merops superciliosus superciliosus</i>	1	1	1	1	1	5	0	2
<i>Hypsipetes m. madagascariensis</i>	1	1	1	1	1	5	0	2
<i>Lonchura cucullata scutata</i>	1	1	1	1	1	5	0	1
<i>Foudia madagascariensis</i>	1	1	1	1	1	5	0	1
<i>Corvus albus</i>	1	1	1	1	1	5	0	4

Recently introduced *Passer domesticus*, *Acridotheres tristis* and *Pycnonotus jocosus* omitted from list. Historical records included (e.g. *Circus maillardi* on Mayotte); *Milvus parasitus* considered not breeding.

1's; the number of such permutations per species is a measure of how much the species deviates from the 'island-size model'. The majority of endemic taxa, most of which are forest species, need several permutations to fit the 'island-size model', while the recent colonizers, most of which prefer open habitat, occur throughout the archipelago (Table 3). In general, small endemic birds (<70g) need significantly more permutations to fit the 'island-size model' than large birds (Table 4; 2-tailed Fisher exact, $P = 0.0011$), meaning that more small birds are absent from larger islands than expected, which is contrary to expectations of island biogeography and viable population concepts.

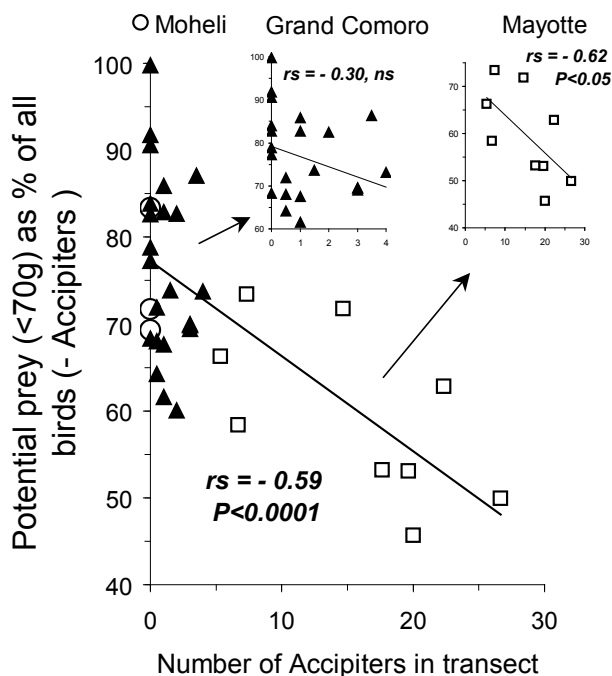


Figure 4. Relationship between Frances's Sparrowhawk *Accipiter francesiae* numbers and the proportion of potential prey in the bird communities in transect-counts on Mayotte, Grande Comoro and Moheli Islands (Comoros).

Table 4. Frequency distribution (number of bird taxa) of the number of permutations needed to fit the 'island-size model' (cf. Table 3) for small (<70g) and large (≥ 70 g) endemic birds on the Comoros.

Weight class	Number of permutations needed	
	0-2	>2
small (<70g)	15	22
large (≥ 70 g)	16	2

1's; the number of such permutations per species is a measure of how much the species deviates from the 'island-size model'. The majority of endemic taxa, most of which are forest species, need several permutations to fit the 'island-size model', while the recent colonizers, most of which prefer open habitat, occur throughout the archipelago (Table 3). In general, small endemic birds (<70g) need significantly more permutations to fit the 'island-size model' than large birds (Table 4; 2-tailed Fisher exact, $P = 0.0011$), meaning that more small birds are absent from larger islands than expected, which is contrary to expectations of island biogeography and viable population concepts.

We quantified 'deficiencies' at the generic level for not introduced, terrestrial species, under the assumption that every genus could be expected to be represented by a similar number of species on each island, except that the Karthala does have a montane zone, lacking on the other islands; Grand Comoro White-Eye *Zosterops mouroniensis*, the single exclusively montane species on the Karthala has been excluded from this comparison. There are e.g. two *Coracopsis* parrot species on the Karthala and Anjouan, one on La Grille and Moheli, and none on Mayotte; consequently, the deficiency is -1 for La Grille and Moheli, and -2 for Mayotte. There are more deficiencies of large birds on small islands which also lack sparrowhawks (La Grille; Moheli), while more prey-size species are lacking on Mayotte (Table 5; Fisher exact test, $P = 0.018$). Anjouan also lacks many small bird species, but historical sparrowhawk abundance is less certain here (see discussion).

The previous analysis does not take into account the important effect of island size and isolation, which affects the probability of colonization by any species. When the number of species in the weight-category of potential prey which currently survive on each island is compensated for island size and isolation, a clear negative relationship with sparrowhawk abundance emerges (Fig.5).

Discussion

Sparrowhawk densities. — Benson (1960) gave an appreciation of Frances's Sparrowhawk densities on the different Comoro Islands: he found it 'unrepresented' on Moheli, 'not at all common' on Grand Comoro, 'far from uncommon' on Mayotte, and 'formerly common, but now practically extinct' on Anjouan (this appreciation was based undoubtedly on the fact that many 19th century specimens are present in collections, see e.g. Knox and Walters 1994). The average density estimate from the point-transect counts in 1993 on Mayotte was 1.25 bird/ha, which, taking into account the low detectability of the species, must still have been an underestimation. The interpretation of the exclusive position of individuals (of each sex) in the mapping and the "trefclus" analysis in 1995 and 1996 indicated (correctly as it turned out later) six or seven pairs in a quarter of the Coconi study plot. However, at the time we were suspicious about the results of such a

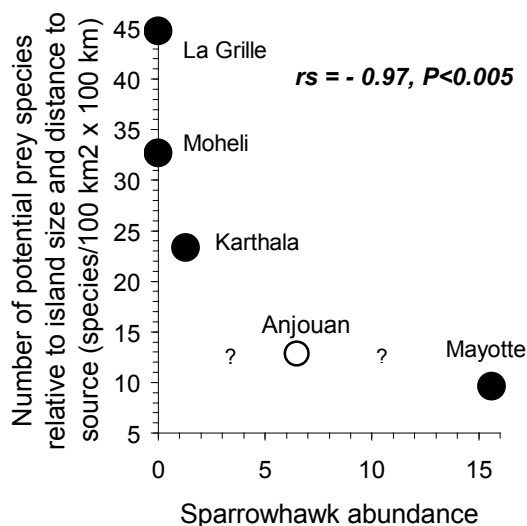


Figure 5. Relationship between Frances's Sparrowhawk *Accipiter francesiae* abundance (number of birds in transect) and the number of potential bird prey species on the Comoro Islands, re-scaled for island size and distance to source population (sparrowhawk abundance on Anjouan is historically uncertain and varied between years, see results and discussion sections).

Table 5. Species deficiencies at the generic level for terrestrial, not introduced birds on the Comoro Islands (excluding montane species).

Genus	Weight class	Grand Comoro		Moheli	Anjouan	Mayotte
		(Karthala)	(La Grille)			
<i>Accipiter</i>	3		-1		-1	
<i>Treron</i>	4	-1	-1			-1
<i>Otus</i>	3		-1			
<i>Coracopsis</i>	3,4		-1		-1	-2
<i>Zoonavena</i>	1			-1		-1
<i>Coracina</i>	2				-1	-1
<i>Hypsipetes</i>	2				-1	-1
<i>Cyanolanius</i>	2		-1		-1	-1
<i>Saxicola</i>	1				-1	-1
<i>Turdus</i>	2					-1
<i>Nesillas</i>	1	-1	-1		-1	-2
<i>Humblotia</i>	1		-1		-1	-1
<i>Nectarinia</i>	1				-1	-1
<i>Dicrurus</i>	3		-1		-1	
Total likely prey	1	-1	-2	-3	-5	-6
Total possible prey	2	0	-1	0	-3	-4
Total no prey	3,4	-1	-5	-3	-1	-3
Class 1&2 as % of all		50	38	50	89	77

high density. The subsequent data from nest counts showed an average territory size of 2.3 ha/pair in the study plots in the wet northwestern sector of Mayotte. The study plot at Mrowalé where nests were counted in 1997/98 was also part of a transect count in 1992-94; we encountered only 'average' numbers of sparrowhawks here, and less than half the numbers found in the two highest transects (Stevens and Louette 1999). This suggests that there might be places on Mayotte (e.g. Ochoungui and Pic Combani) with breeding densities of Frances's Sparrowhawks approach 1 pair/ha.

Like in the Eurasian Sparrowhawk (Newton 1986), the finding of nests is the best method to study the population and spacing of the Frances's Sparrowhawk, and it is surprising how easily the birds are overlooked, even in this exceptionally confiding species; this aspect, and the consequent underestimation may apply to other studies which have not used comprehensive nest counts for density estimations. The regular spacing of nests (Fig. 1) suggests that the species is strictly territorial (Marquiss and Newton 1982, Newton 1989); occasional observations of a marginal overlap in individual hunting ranges (Herremans *et al.* 2001), would not invalidate this concept, because it is also found in other truly territorial accipiters (Newton 1986, Bijlsma 1993). Difficulties in locating adult pairs which showed no breeding activity (either not breeding or having suffered nest-loss early in the breeding season) suggest that the densities presented in Fig. 1 may still be a slight underestimation. The positive skew and tendency for a secondary peak in the graph of the nearest-neighbor distances at about twice the minimal inter-nest distance also suggests that some pairs or nests may still have been overlooked (Fig. 2: skewness=1.48, SE=0.62). With an average fledging success of 1.5 young per initiated nest (Herremans *et al.* 2001), the density in the humid sector of Mayotte is minimally 150 sparrowhawks/km² by the end of the breeding season. Immature birds can be recognized by plumage up to two years after hatching (Herremans *et al.* 2001), but no such birds were observed attending nests. This indicates that the high densities were not due to exceptionally favorable conditions with a rapidly expanding population, which is normally based on increased recruitment with high percentages of young birds taking part in breeding (Reese and Kadlec 1985, Newton 1986, Bijlsma 1993). Using mortality rates as in the Eurasian Sparrowhawk (55% during the first year, 40% in the second and 30% yearly thereafter in adults: Newton *et al.* 1983, Bijlsma 1993), 26 recruits would be needed per km² in the Frances's Sparrowhawk to keep the population stable on Mayotte, but from our studies only 17 would be available by the end of the second year. Clearly, either mortality is lower on Mayotte than assumed from the example of the Eurasian sparrowhawk, or more young fledge on average than noted during our study. With mortality rates at 45% in the first year, 30% in the second year and 20% in adults, and no recruitment in the first two years, there would be a surplus and the number of floaters would become about 80 birds/km², which would bring the total population to 230 birds/km² (0.43 ha/bird) by the end of the breeding season. There are, however, indications that birds may disperse from the high-density breeding areas to the drier parts of the island, and part of the floating population might spend time outside the main breeding areas (Herremans *et al.* 2001).

As far as we could establish from quantitative or qualitative information in the literature, the presently documented breeding densities of Frances's Sparrowhawks on

Mayotte Island are by far the highest documented for any *Accipiter* in the world, and possibly for any strictly territorial raptor (compare Thiollay 1975, 1993, Cramp and Simmons 1980, Blakers *et al.* 1984, Forsman and Solonen 1984, Newton 1986, 1989, Patrimonio 1987, Aumann 1989, Brazil and Hanawa 1991, Bühler 1991, Bijlsma 1993, van Balen 1994, Galushin *et al.* 1996, Tomialojc and Wesolowski 1996). However, a valid ecological comparison for the Frances's Sparrowhawk on a Comoro Island is difficult to find. There appear to be only seven *Accipiter* species in the world in its size class <250g with reptiles as a major part of the diet: *francesiae*, *butleri*, *imitator*, *badius*, *brevipes*, *soloensis* and *trinotatus* (del Hoyo *et al.* 1994, Ferguson-Lees & Christie 2001). Frances's Sparrowhawks are qualified as "very common" on Madagascar (Rene de Roland & Thorstrom 2003), but no comparable quantitative data are available (Rands 1936, Wattel 1973, Langrand and Meyburg 1984, Langrand 1990, Thorstrom and Watson 1997), other than the statement that the distance between nests of the same pair in successive years was on average 105 m (range 0-250 m) (Rene De Roland 2000). *A. badius* occurred at 1-2 pairs/100 km² and at nearest-neighbor distances of 4.7 km in study areas in South Africa, where it co-occurs with six other *Accipiters* (Tarboton 1978, Tarboton and Allan 1984). In woodland areas of West Africa, where it is the only species in the genus, 26 pairs/100 km² were found in the Ivory Coast (Thiollay 1975), and 1 pair/1.2 km² in Nigeria (Smeenk and Smeenk-Enserink 1977). It is the commonest *Accipiter* in Guinea (Rondeau *et al.* 2008). This species however does not occur on any of the circum-African islands, but is qualified as 'the commonest small hawk, found almost everywhere' on Sri Lanka (Henry 1955). Two of these seven *Accipiter* species are migrants: *brevipes* has been recorded to breed at 17.3 pairs/100 km² (Galushin *et al.* 1996), but no density estimates of *soloensis* in its breeding quarters were found (Choi *et al.* 2008 say it used to be common in Korea). The sixth species, *trinotatus*, is said to be common on Sulawesi (del Hoyo *et al.* 1994). On other Indian Ocean Islands, two endemic Kestrels became specialists of reptiles: Seychelles Kestrel *Falco araea* on Mahé (Seychelles) occurs with 7 pairs/km² (recalculated from Feare *et al.* 1974) at an unusually high density for a kestrel, while Mauritius Kestrel *F. punctatus* on Mauritius is now recovering after having been at the brink of extinction, with the densities in historical times unknown (Jones 1987).

At comparable densities to its ecological counterparts, there would be place for 4-312 pairs of Frances's Sparrowhawks on Mayotte only. The breeding population on Mayotte can at present preliminary be estimated in the order of magnitude of 7,225-10,960 pairs, using figures of 35-50 pairs/km² in 175 km² of the wettest northwestern section of the island (but assigning the coastal strip to the next category), 10-20 pairs/km² in 110 km² of a drier zone in the east including the Choungui massif (assigning the coastal strip to the next category), and 0-0.1 pairs/km² in 89 km² of the dry southern part (excluding the Choungui massif), along the coast in the east, and in habitat rendered unsuitable by too extensive clearing (delimitations of abundance-zones based on Louette *et al.* 1993b, Stevens and Louette 1999).

On Grand Comoro, Frances's Sparrowhawks are about ten times less frequently encountered in suitable habitat than on Mayotte (Louette *et al.* 1993b), and breeding densities may therefore be in the order of magnitude of 20 ha/pair in suitable areas. We

did no standardized transect-count on Anjouan ourselves, but the daily reporting rates (including the data from C. Marsh from 2005) indicate that the abundance on Anjouan is at present of the same order of magnitude or slightly lower than in suitable habitat on Grand Comoro. Anjouan has the highest human population density of the Comoros, with the longest period of settlements in the interior, where people are dependent on the terrestrial system for all their requirements. The island has been severely transformed in recent times, leaving little original forest vegetation and with substantial areas cleared of tall vegetation, which has probably also fundamentally affected birdlife. Both sexes of the subspecies *pusillus* from Anjouan have masculine plumage (Benson 1960, Louette 2000) and in view of the generally positive relationship between neoteny and density (Louette *et al.* 1993a), it is unlikely that sparrowhawk densities would historically have been as high on Anjouan as those of the neotenic form *brutus* on Mayotte. We use therefore for the following discussions a historical sparrowhawk abundance on Anjouan greater than that on Grand Comoro but smaller than on Mayotte.

Sparrowhawk numbers may fluctuate; contemporary abundance does furthermore not necessarily reflect abundance in historical times. In stable environments, however, raptor populations tend to be remarkably stable (Newton and Marquiss 1986, Newton 1991). In general, forest bird numbers did not fluctuate greatly on Mayotte (Louette *et al.* 1993b, Stevens and Louette 1999). We believe that the order of magnitude of contemporary abundance was appropriately captured by the transect counts, most of which represent the average of up to three repeats. Historical abundance will inevitably remain undocumented, but because Frances's Sparrowhawks co-evolved with the lush indigenous forest vegetation on the Comoro Islands, contemporary density estimates in this vegetation may be the best approximation one can make about the order of magnitude of the historical density. Only if significant niche expansion would have taken place, to which insular forest birds may be particularly partial (Blondel *et al.* 1988, Thibault *et al.* 1992), would densities in forest edge or in open landscapes be higher than in the primary habitat. Our data from Mayotte show similar sparrowhawk densities in forest and forest-edge habitat (Stevens and Louette 1999). Anjouan is more problematic in judging historical densities, and Benson's appreciation based on the number of early specimens is the best available.

Do sparrowhawks affect the bird communities on Mayotte ?— With Mayotte holding the highest breeding density of a sparrowhawk in the world, would there be any impact on the bird communities ? Generally, predator numbers follow those of prey populations. In the Eurasian Sparrowhawk, higher densities correlated with higher prey indices (Newton *et al.* 1986) and there was inconclusive evidence for effects of changing sparrowhawk populations on prey abundance (Newton *et al.* 1997), except in the immediate vicinity of the nest (<60 m), where prey-bird populations were depressed (Newton 1986). With the presently documented high densities on Mayotte, the entire sparrowhawk territory becomes the 'immediate vicinity of the nest' and impact on prey populations may be expected over most of the island, except the drier parts, where sparrowhawks are sparse (Herremans *et al.* 2001).

The choice of weight-categories of prey species was based on data from: (1) the

Eurasian Sparrowhawk which takes 92% of all prey smaller than 55% of its own body weight in the British Isles (Newton 1986), while about 90% of its prey items weigh <50 g in Europe (Bühler 1991, Bijlsma 1993), and (2) the Sharp-shinned Hawk *Accipiter striatus* in which >90% of prey is <50% of its body weight (Storer 1966, Reynolds 1972). The cut-off of 70g we used for Frances's Sparrowhawk is 56% of its average body weight. However, the previous two sparrowhawk species are specialized bird hunters, while the mainly reptilivorous Shikra seems to take only small birds (Smeenk and Smeenk-Enserink 1977, Tarboton 1978). Birds below 20 g therefore are the most likely to fall victim to Frances's Sparrowhawk, while class 2 (20-70g) is still considered to be within the potential prey range. Class 3 (70-<150g) may only exceptionally be taken as prey, and birds over 150g are unlikely to be taken (see also Herremans *et al.* 2001). Potential-prey size birds (<70g) were expressed as a percent of all birds, excluding Accipiters (ignoring the possibility of cannibalism) for comparisons of prey abundance between islands. This measure is better buffered against stochastic effects than the numbers of birds observed (see e.g. the effects of an encounter with a bird party). It facilitates comparisons between islands because differences in conspicuousness could affect numbers counted, e.g. because different species, habitats and maybe shifts in breeding seasons could interfere with inter-island comparisons.

Frances's Sparrowhawks are catholic in their food choice and take a variety of small vertebrates (reptiles, birds, rodents), large insects and occasionally carrion, though sparrowhawks on Mayotte have a much larger proportion of reptiles in the diet than on Madagascar (Herremans *et al.* 2001). The central toe is short in the Frances's Sparrowhawk, which therefore belongs to the *brevipes*-type, indicating that it is not a specialized bird hunter, but potentially omnivorous, capturing most prey by pouncing, not aerial pursuit (Wattel 1973, Herremans *et al.* 2001). Reptiles, most particularly skinks *Mabuya comorensis* and green gecko's *Phelsuma sp.*, are the staple food on Mayotte. Green geckos have radiated on Mayotte into three endemic species, and two more species became established in recent history (Losos 1986, Meirte 1994). With five species, niche partitioning and specialization of the *Phelsuma*'s on Mayotte can be expected to have resulted in a high overall density and biomass in the wet sector. Anecdotal information seems to confirm this: several tens of gecko's were found when a single tree was felled, and it is not uncommon to observe up to ten *Phelsuma*'s from a single vantage point (D.Meirte unpubl. data). The only indication that sparrowhawk numbers follow biomass of gecko's on Mayotte may come from the preference of both for the wettest zone of the island, while both are uncommon in the drier parts, and absent from the small islets around Mayotte (Herremans *et al.* 2001, D. Meirte unpubl. data). On Praslin Island in the Seychelles, the highest lizard biomass was also found in native forest on higher ground (Evans and Evans 1980). The inverse relationship between the abundance of prey-size birds and sparrowhawk numbers (Figs. 2-3, Table 2) is compatible with the proposition that the exceptionally high abundance of Frances's Sparrowhawks limits the numbers of small birds on Mayotte. Bird counts on Mayotte were aimed at studying forest bird communities (Louette *et al.* 1993b), and there were no transects in the dry eastern and southern coastal areas, nor on the eastern islet Pamandzi (Petite Terre), where sparrowhawks are only observed occasionally (Herremans *et*

al. 2001), but where small birds are strikingly abundant. Including the results from transects from areas on Mayotte with few sparrowhawks is expected to strengthen the relationships in Figs. 3-4. There is no evidence at all from hunting behavior, territorial pressure, time allocation or breeding success for any food shortage for sparrowhawks on Mayotte (Herremans *et al.* 2001). Although hunting is opportunistic, reptiles are the staple food of Frances's Sparrowhawks on Mayotte, similar to specialization in other endemic small raptors on Indian Ocean Islands (e.g. Seychelles Kestrel (Watson 1992) and Mauritius Kestrel (Jones 1987)). It is, however, possible that birds, if available, would be preferred as prey, possibly because hunting the generally heavier bird is more profitable for a similar energy expenditure; furthermore, although by far less common compared to reptiles, a bird may simply be more conspicuous to an opportunistic hunter than the more cryptic reptiles and the proportional impact on the numbers of birds may thus be higher, even though they do not figure very high in a study of prey numbers (Herremans *et al.* 2001). There are examples from New Zealand, where predators with mammalian staple food had severe impact on bird numbers only when the predator population became high as a consequence of changes in the staple food (Taylor 1979, Griffin *et al.* 1988). Lizard populations seem generally to be rather stable (Schoener 1985), including *Mabuya* and *Anolis* species, the latter being ecologically similar to *Phelsuma*. There is nevertheless some evidence from the Seychelles, that numbers of green gecko's, or at least their apparent availability to a predator, may fluctuate considerably (Watson 1992), in which case sparrowhawks could temporarily become more dependent on alternative prey. A depressing effect by predators on the population levels of alternative prey is not uncommon, particularly in simplified ecosystems, such as small oceanic islands with depaupered faunas. Where population levels of predators are maintained by an abundant staple food, any decline of this prey basis forces the predators to switch to alternative prey: classical examples are the lemming-fox-wader cycles in the arctic (Summers 1986, Summers and Underhill 1987, Syrouchkovskiy *et al.* 1991), the hare-goshawk-grouse cycles in North America (Keith and Rusch 1988) and the studies where experimental removal of predators made population levels of secondary prey to increase (Newton 1991). Whether it is a seasonal fluctuation in the staple food, a preference for birds or merely their conspicuousness that makes bird numbers depressed in parallel to sparrowhawk numbers on Mayotte remains unknown. Direct suppressive predation remains a possibility (Kenward and Marcström 1988), but with the present data, effects of direct predation can not be distinguished from an effect of predation risk avoidance and prey refuge use (Mittelbach and Chesson 1987, Sih *et al.* 1988, Meese and Fuller 1989, Sodhi *et al.* 1990), which could be an alternative explanation for the higher abundance of small bird species in areas with fewer sparrowhawks. In any case, 'prey refuges' in an insular situation inevitably also reduce effective island and population size, and therefore probably increases the risk of extinction. A direct relationship between low survival rate and high extinction risk was demonstrated for insular birds on Barro Colorado Island (Karr 1990), and the effects of introduced predators on island birds are well known (Griffin *et al.* 1988). Reduced survival rates under increased predation pressure by high numbers of sparrowhawks may also be the mechanism that has driven to extinction (or prevented establishment)

on Mayotte some species common elsewhere in the region. A situation with a rather similar outcome has been documented for an intermediate trophic level in the Bahamas, where abundant predatory lizards limited the numbers of individuals and species of spiders (Schoener and Toft 1983, Toft and Schoener 1983, Schoener and Spiller 1987, Spiller and Schoener 1988). The negative effects of lizards on the establishment of invading spiders have been experimentally demonstrated in this case (Schoener and Spiller 1995).

There are only limited data on density for bird communities from mainland Madagascar (e.g. O'Dea *et al.* 2004, Watson *et al.* 2004, Scott *et al.* 2006) at hand, and therefore it remains impossible to assess whether the sparrowhawks on Mayotte depress bird populations below the densities found on the adjacent "mainland", or whether even these high sparrowhawk densities can not undo the density inflation effect which is part of the insular syndromes affecting small insular birds. Several small birds are certainly less common on Mayotte than on other Comoro islands (Stevens and Louette 1999). However, if the densities of small birds on Mayotte were still higher than on the mainland, despite the sparrowhawks, the 'low predation' theory which has been invoked to explain higher densities of insular populations (Faeth 1984, George 1987), may need modification.

May sparrowhawks have shaped Comoro bird faunas in evolutionary terms ? — Three distinctly different subspecies of the Frances's Sparrowhawk have evolved on the Comoro Islands, and their presence on the islands is therefore certainly historic. Colonization of an island by any bird is dependent on the success of a fragile founder population, most probably arriving in very low numbers and being dependent on long survival in order to find the right habitat and improving the chances to encounter a mate. Under such conditions where the presence and survival of an individual is fundamental, the impact of a high sparrowhawk population on the island can be decisive. Newton (1986) e.g. predicted from the high elimination rate of escaped budgerigars by Eurasian Sparrowhawks in Scotland that the latter would be efficient at preventing the former from becoming established, and generalized that rare and easily caught species may be eliminated by sparrowhawks that thrive on an alternative staple food.

The Comoro bird faunas have a number of as yet unexplained anomalies (Louette *et al.* 1989, 1993b, 2008). Particularly Mayotte and Anjouan have too few species, especially small birds (Louette 1988, Fig.5, Tables 3-5). Small birds deviate more from the 'island-size model' than large birds, meaning that, at odds with expectations, more small birds had difficulties either to colonize or to maintain viable populations on larger islands. The anomalies are particularly striking on islands with sparrowhawks (Tables 3,5). Some species which are absent or have only one species on Mayotte and Anjouan, but sometimes two on other islands (including on the smallest islands), are widespread in the region and common in a variety of habitats (*Nesillas*, *Nectarinia*, *Turdus*, *Hypsipetes*: Louette and Herremans 1985, Louette *et al.* 1988b), indicating that they are good colonizers and opportunists. The absence of several species from Mayotte and Anjouan is even more remarkable in zoogeographical terms because these islands are larger and closer to Madagascar, the main source area than is the small

island of Moheli, which is richer in species, but lacks a sparrowhawk (we do not take into account here the possibility that Grand Comoro itself may have acted as a source for some species: Louette 1996a). The position of Anjouan in Fig. 5 is uncertain, both in terms of historical sparrowhawk abundance (see above), and maybe also in terms of the number of small bird species presently remaining: if any species became extinct recently because of habitat destruction by humans, Anjouan would shift upwards in Fig. 5. There are furthermore anomalies of distribution and inexplicable scarcity on Mayotte, whereby species (e.g. Forest Fody *Foudia eminentissima*, Mayotte Sunbird *Nectarinia coquereli*, Madagascar White-Eye *Zosterops maderaspatana*) in genera that prefer altitudinal forest vegetation on other islands are more abundant at lower altitude, and in the drier and less lushly vegetated parts of Mayotte (Louette *et al.* 1989, 1993b, Stevens *et al.* 1995, Stevens and Louette 1999, Table 5), where Frances's Sparrowhawks occur only marginally (Herremans *et al.* 2001). The House Sparrow *Passer domesticus* occurs all over Moheli, where there is no *Accipiter*, but is restricted to towns in the drier, coastal areas of Mayotte and Grand Comoro (Louette 1988), which are not frequented by sparrowhawks.

In conclusion, past evolutionary processes remain inevitably speculative and can not be confirmed by experimentation, yet contemporary evidence from bird distribution and abundance, and historical evidence from the lower rate of successful colonization are all compatible with the hypothesis that the record abundance of Frances's Sparrowhawks on Mayotte (and possibly also on Anjouan) have substantially affected the prey-bird communities, either directly by predation or indirectly through predation avoidance on an island with insufficient prey refuges. The sparrowhawk predator effect hypothesis can account for a number of the too many as yet unexplained zoogeographical anomalies on the Comoros. Theoretically, the ultimate test could be to translocate neotenic sparrowhawks from Mayotte to Moheli, but in view of the high level of endemism among potential prey species on Moheli and the predicted impact by sparrowhawks, such would not be a good idea for conservation. More in general, we would like to argue against the translocation of insular predators (in fact of any trophic level) with a clear potential for density inflation to places with endemism.

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A preliminary vertebrate palaeontological cave survey of the Comoros Islands.

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Abstract.— The results of a reconnaissance palaeontological cave survey are described, with an island by island review of potential fossil localities within the Comoros Archipelago. Lava cave localities were examined and details recorded. The first lava caves on Anjouan were recorded, including new native bat roosts. In general the cave localities were too eroded, lacked any substantial sediment deposits or were geochemically unsuitable for the long-term preservation of fossil material; hence the lack of success in finding a single preserved fossil or subfossil bone.

Keywords — Anjouan, Mohéli, Grande Comore, Mayotte, cave, fossil, bat, terrestrial snail

Introduction

The Comoros Archipelago (Fig.1) comprises four main volcanic islands situated between Mozambique and Madagascar at the north end of the Mozambique Channel. Estimated ages for the islands, based on the Somali Plate Motion and Mount Karthala active volcano, are 7.7-10 MYA for Mayotte, 5.0 MYA for Mohéli, 3.9 MYA for Anjouan, and 0.5 MYA for Grande Comore (Emerick & Duncan 1982; Harris & Rocha 2009). Running from east to west, the most easterly and oldest is Mayotte (local name, Maore), followed by the smallest Mohéli (Mwali), then Anjouan (Ndzuani), while the largest, youngest and most westerly island is Grande Comore (Ngazidja). The islands are entirely volcanic in origin, and have never been connected to any continental landmass or to each other. Grande Comore has an active volcano, Mt Kathala, which is considered to have one of the largest craters in the world (Pavlovsky & Saint-Ours 1953). Surrounding coral reefs only occur on Mayotte, but are not extensive and virtually no lagoonal systems exist. The islands have a complex social history. The initial colonisation was first by Africans, then Austronesians (proto Malagasy) settlers in the 6th century, followed by Arabians c. 8-10th centuries until the 15th century (Newitt 1983; Allibert 1984; Dick-Read 2006), and since then a mixture of African, Arabic and French. Despite the Portuguese having been aware of the islands since 1505 (Toussaint 1966), little early literature has survived. The first faunal accounts did not appear until the late 16th century (Allibert 1984; Liskowski 2000; Cheke 2010), by which time the islands' resources had already been heavily exploited.

The islands of the Comoros Archipelago lack an existing fossil record and appeared to be ideal candidates for a palaeontological survey; thus the main aim of this reconnaissance was to determine whether fossil material was preserved. Cave surveys were considered the best option to achieve this aim, as marsh and sand dune sites are virtually absent. Each island was surveyed dependant on age, the steepness of the terrain,

presence of depositional basins and the geomorphology of the cave systems.

Methods

In April/May 2009, we undertook a brief (due to limited resources and time) reconnaissance survey of all of the main Comoros Islands. Logistically, cave localities were reasonably easy to access but, politically, difficulties arose, as access to some required extensive negotiation with local land owners and the obtaining of special permits. Cave sites that had previously been mapped were relocated using GPS, while new and unexplored caves were located by asking local land owners and assistance from Action Comores. This proved particularly productive on Anjouan. Terrestrial snail shells were sought after, as their presence has been shown previously to be an important indicator for finding vertebrate remains (Hume 2004). We allotted 9 working days for Grande Comore and Anjouan and 2 days for Mayotte (for Moheli see Middleton (1999)). Results are presented here, together with comments on the potential of other localities to yield fossils within the archipelago.

Navigation was facilitated by 1:50,000 topographic maps of each island (the French Institut Geographique National series). Minimal tools were taken for preliminary research; these included caving lights, small trowel and fork, collecting bags, compass, inclinometer, GPS unit, laser measuring device and photographic equipment. Non-destructive palaeontological methods were employed in order to disturb localities as little as possible. Due to the logistics involved, other equipment, e.g. fine sieving apparatus, was not taken.

Results

Grande Comore

Grande Comore is the largest island (67 x 27 km), with a total surface area of 1,148 km². The island is characterised by two volcanoes, the extinct and heavily eroded La Grille in the north, with an elevation of 1087m, while in the south the still-active Mount Karthala rises to a height of 2,361 m. As Grande Comore is a very young island, soil development is poor, the terrain generally rocky and water catchment areas almost non-existent. Water run-off is high, exacerbated by severe deforestation and soil erosion. There is virtually no surrounding coral reef or lagoon. Many lava caves were documented by Middleton in 1997 and 1998 (Middleton 1998a, 1998b, 1999, 2005).

Panga Betini HH7-10-11 (Betini Cave) [S 11°31.840' E 43°17.198']

Just north of the airport on the west side of the island, north of the capital, Moroni, lies a series of lava tube caves. These are clearly developed in the relatively recent lava flows visible down the flanks of Mt Karthala. This area is known as the Hahaya Cave Area (Middleton 1999, 2005), and comprises a number of long lava tube caves with occasional roof collapses. The caves are situated in an undulating lava plain covered with sparse, stunted vegetation broken only by an occasional Baobab tree (*Adansonia* sp.). Taller plants grow in the sheltered environs of cave roof collapses and are good indicators of potential cave openings. Access to Panga Betini was achieved by climbing

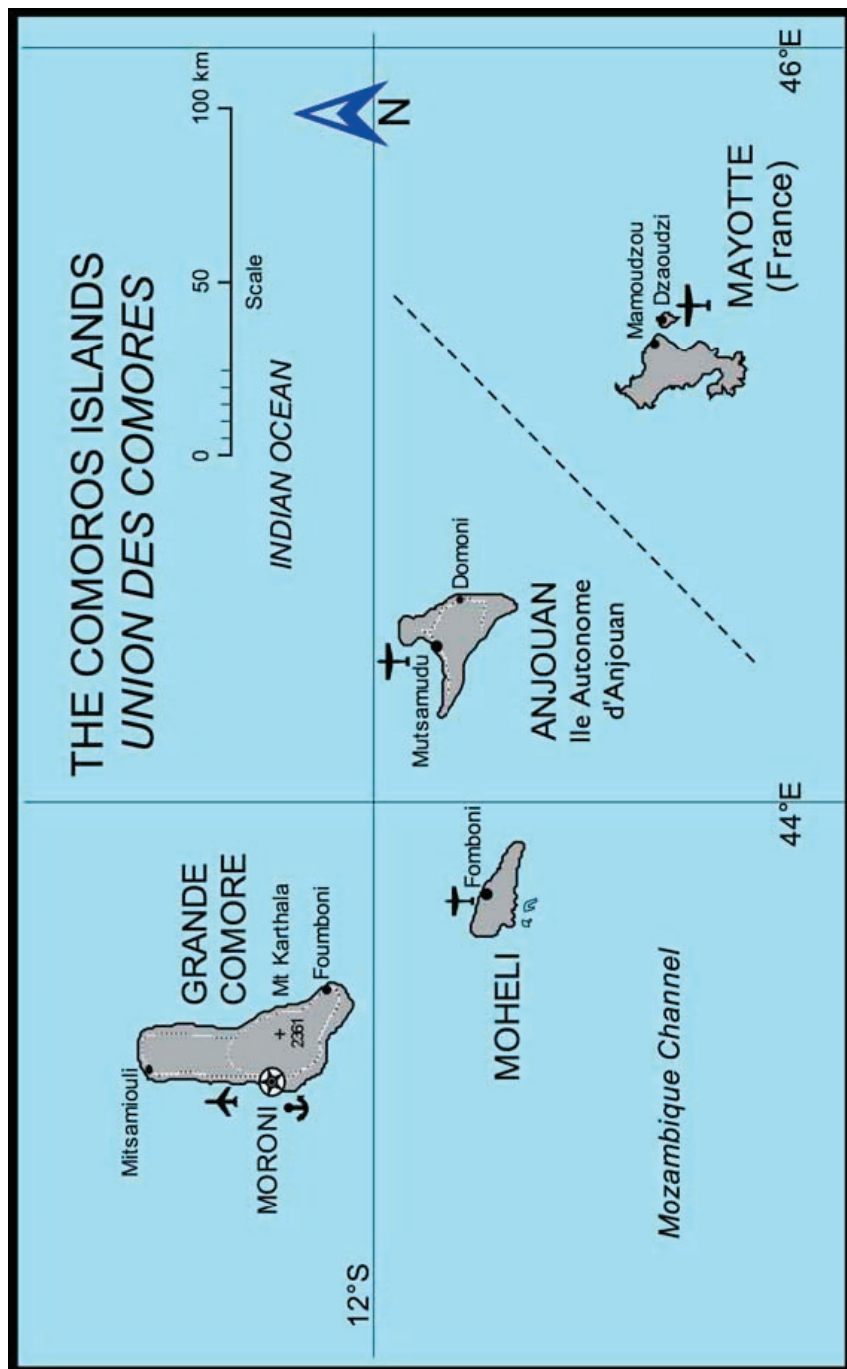
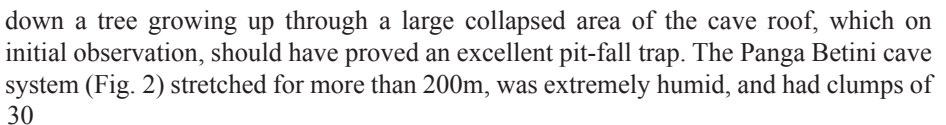


Figure 1. Map of the Comoros Archipelago.

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tree roots hanging from the roof ceiling. The cave floor was strewn with thick (1 m+) cave breakdown boulder scree (Fig. 3), with virtually no sediment. Skeletal elements of domestic cattle *Bos* sp., goat *Capra* sp. and rat *Rattus* sp. were discovered in the entrance, but were already in a serious state of decay, being fragile and exhibiting severe (>70%) bioerosion. No bones or snail shells of any native species were discovered.

Cave HH12-13

This cave (Fig. 2) was 180 m long, with a central large 7m pit. Examination was mainly carried out around the pit area and, similarly to Panga Betini, the cave floor was covered with cave breakdown - rocky scree up to 1 m thick. Removal of rocks and digging down the sides of the cave wall produced almost no sediment. The cave was humid and damp and terrestrial snail shells were absent. No bone material was discovered.

Coastal cliff caves

Just north of the airport, a series of sea caves were visible when flying overhead. Access was obtained by getting permission from airport security, as the airport light beacon was in the vicinity of the cliff edge and out of bounds to the general public. The cliffs were sheer and approximately 50m in height. Comparatively fresh basalt formed a flow surface platform at the base of the cliffs. Large sea caves with surface connections had been eroded out by the action of the waves and were devoid of any floor debris.



Figure 3. Main passage in Ngama Betini, Grande Comore.

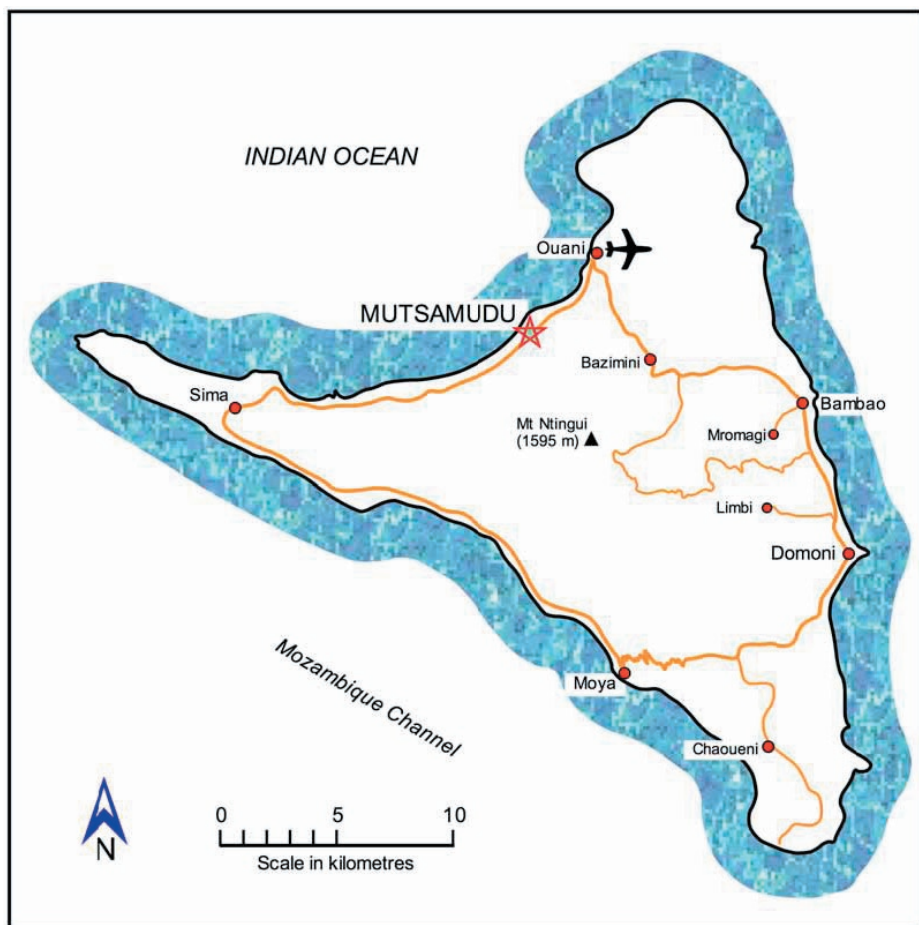


Figure 4. Map of Anjouan, detailing major roads and localities mentioned in the text.

Fossil potential of Grande Comore caves:

Low to Moderate. Grande Comore caves proved unproductive. This is almost certainly due to the young age of the island and the lack of sediment in the cave systems. Due to the size of Grande Comore and the large numbers of lava flows, many more cave systems must exist, but they are likely to be taphonomically similar to those investigated. The absence of preserved snail shells indicates also that long-term preservation of fossil material is unlikely. Marshes are almost non-existent, but an area stated as being a potentially interesting marsh locality in the south of Grande Comore, but without road access, should be investigated by a future team with more time available.

Anjouan

Anjouan (Fig. 4) is approximately 40 km long and covers an area of 424 km². The island has three mountain chains, Sima, Nioumakele and Jimilime, which originate

from the central peak, Mtingui, at 1,595 meters. This gives Anjouan its distinctive triangular shape. The island is steep and dissected by numerous river systems that produce waterfalls in the wet season. Being one of the older islands, soil cover is deep, but severe deforestation and over-cultivation has caused serious erosion. A coral reef is situated close to the shore, but is in serious decline due to soil run-off.

Chaoueni Sea Cave *[S 12° 21.683' E 44° 29.678']

This cave is situated on the coast below the village of Chaoueni, and from a distance looked like a classic sea cave. Unfortunately, we were prevented by a local official from actually accessing it, so the true nature of this site remains unknown.

*These coordinates are for the nearest point to the cave that we could reach.

Moya Sea Cave [S 12° 18.564' E 44° 26.094']

The coastal village of Moya has a rubbish-strewn pebble beach below a run-down hotel. To access the cave required walking from the sandy public beach across a lava rock-platform. It is a sea cave about 20 m wide, but shallow (~6 m) with no sediment and devoid of any faunal remains.

Ngama Gombeni [S 12° 10.827' E 44° 26.801']

Behind the village of Bazimini is the large lava tube cave called Ngama Gombeni (Fig. 5), which proved to be the first true lava cave we were able to discover on Anjouan (We used the term 'ngama' or 'pit' because, we believe, this applies to a cave that goes down, rather than in horizontally). The entrance is approximately 3 m x 4 m and is situated on the side of a steep gorge. The cave floor is 2 m below the entrance, blocked by sediment in the direction of the gorge, but with a sharp descent for approximately 60 m in the opposite direction. The passage below the entrance was strewn with ceremonial objects including pottery. The descent to the bottom of the cave was difficult due to large amounts of bat guano, exacerbated by a wet surface from the constant dripping of water from the cave ceiling (Fig. 6). The microchiropteran bats were clearly visible and at least 3 species were present, *Taphozous mauritanus* Geoffroy, 1818, *Myotis anjouanensis* Dorst, 1960, and a third unidentified species. At its lowest point the lava tube appears to be sealed and the floor is completely covered in a large, slimy pool of guano. Humidity was high, so the chances of finding any fossil remains appeared bleak. Some test pits were dug, but the sediment comprised saturated silts and clays, high in organic material and crawling with cave crickets *Ceuthophilus* sp? and unidentified cockroaches. Unsurprisingly, no fossil remains were discovered.

Ngama Mapoudrou [S 12° 12.377' E 44° 30.049']

Heading inland from Bambao, is Mromaji or Mromagi village. Upslope from the village, after a long uphill hike, is Ngama Mapoudrou (Fig. 7), a classic lava tube cave with a terminal clear pool or sump at the base situated approximately 30 m inside. The tube slopes steeply down and has comparatively smooth walls; the floor is partly covered with guano, and it hosts the usual entourage of crickets and cockroaches. Unlike Ngama Gombeni, *Taphozous mauritanus* dominates the microchiropteran fauna. Cave

NGAMA GOMBENI

BAZIMINI AREA

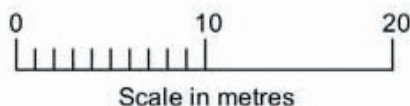
ANJOUAN I., COMORES



SSS Map No. 2054

KEY

- rockfall, boulders
- direction of downslope
- height of roof (m)



Cave length: 65 metres
Average slope angle: -12°

Surveyed by Greg Middleton and
Julian Hume 20 April 2009
using prismatic compass, inclinometer
and Disto A3

Drawn by Greg Middleton 10 May 2009
using Microsoft Excel and EasyDraw 3.0
on an Apple Macintosh
© G.J. Middleton 2009

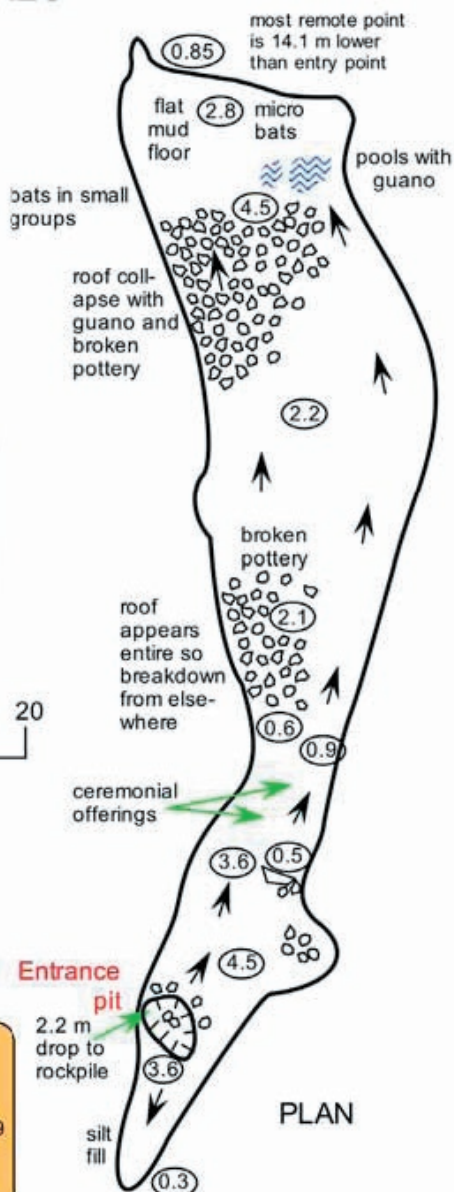


Figure 5. Survey plan of Ngami Gombeni.



Figure 6. Guides and bats in Ngama Gombeni, Anjouan.

breakdown was at a minimum, with virtually no sediment, so no subfossil remains were recovered.

Rousettus Overhang [S 12° 14.481' E 44° 29.773']

There is some confusion about the locality of this cave. According to Sewall *et al* (2003) it was called 'Hi Ros' and described as a cave with an entrance 1 m x 0.5 m, situated behind a waterfall of an intermittent stream, and located at an altitude of 600m. The Rousettus Overhang (Fig. 8) which we visited may, or may not, be the cave to which they are referring. The overhang was located after a very steep climb above the village of Limbi, just north and inland of Domoni. The cave's altitude was measured at 360 m, but this may have not been entirely accurate due to the sometimes erroneous GPS altitude readings. The cave itself was a large overhang 12.4 m high, 15 m deep and about 30 m wide, with a large waterfall to the side. A large pool had formed beneath the waterfall, but the overhang base comprised rocky scree and bat guano. Approximately 2000+ *Rousettus obliviosus* Kock, 1978, fruit bats occupied the overhang ceiling, an unusual roost site for a fruit bat – except that this species, being capable of echolocation, prefers cave sites (Sewall *et al* 2003). This colony may be one of the largest on Anjouan and an important conservation site, as *R. obliviosus* is considered near-threatened on the Comoros (Sewall *et al* 2003; Louette *et al.* 2004).

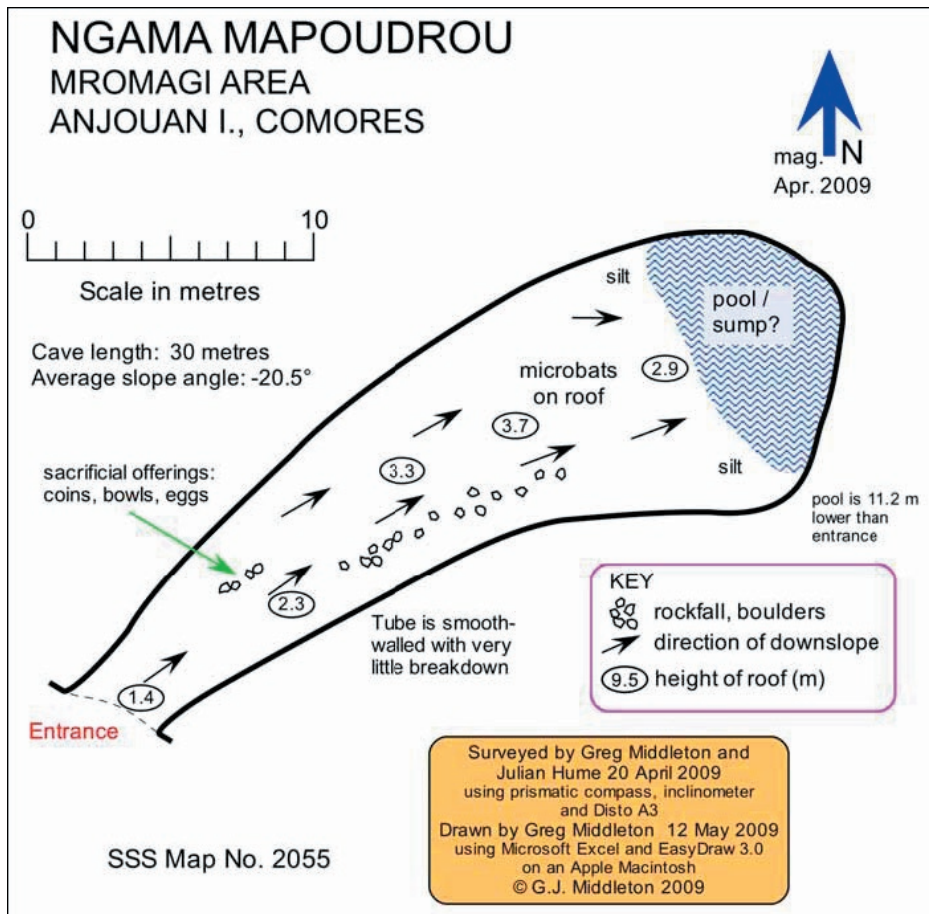


Figure 7. Survey plan of Ngama Mapoudrou cave.

Fossil potential of Anjouan caves:

Extremely poor. Like Grande Comore, Anjouan caves proved palaeontologically unproductive. Few caves evidently exist on the island, and those that do are home to large numbers of bats with associated guano, while infilling from erosional soil runoff artificially increases the depth of sediment and steep cave slopes with constant hydrological influx would remove any vertebrate material before burial. The caves are humid, sediments likely to be similar chemically to other basaltic oceanic islands, e.g. Mascarenes, with higher alkaline pH values (7.5-8) (Hume 2005), and so chemical decay would also prevent the long-term preservation of vertebrate material.

Mohéli

Mohéli is the smallest of the four islands and has a central mountain chain peaking at 860 m. The island is 30 km long and 12 km wide, covering an area of 290

ROUSETTUS OVERHANG

LIMBI AREA

ANJOUAN I., COMORES

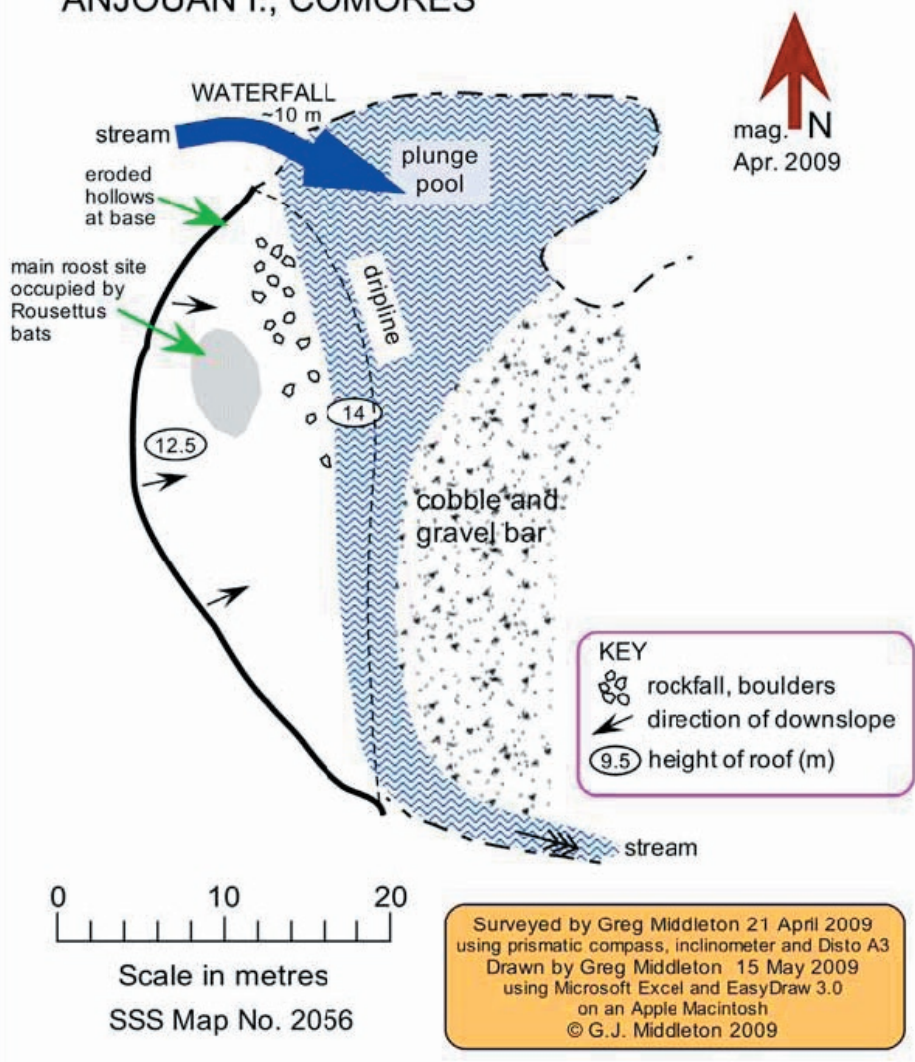


Figure 8. Survey plan of Rousettus overhang.

km². Mohéli has comparatively large tracts of surviving rain forest, but human pressure is severe. Like Anjouan, the island has numerous rivers and streams; soils are deep, but erosional runoff is polluting the surrounding coastal areas.

Fossil potential of Mohéli:

Extremely poor. No caves were found on Mohéli (see Middleton 1998, 2005), despite extensive searching and questioning of the local community. If any do exist, the same taphonomic conditions as Anjouan would probably apply; thus they would not contain any vertebrate fossil material.

Mayotte

Mayotte is the oldest of the Comoros Islands, is 39 km long by 22 km wide and covers an area of 375 km². As it is the oldest, it is also the most eroded, with the highest peaks only reaching between 500 and 600 m above sea level. Another indicator of its considerable age is the presence of a well developed coral reef system which encircles almost the entire island. There are a number of large islets within the lagoon, the principal being Dzaoudzi and Le Pamanzi. Mayotte is administratively part of France and has a significant tourist industry; thus deforestation and pollution are much less apparent than on the other islands which form the Union des Comores.

Grande Terre sea cave

A large sea cave was visible during the boat trip from Dzaoudzi to Grande Terre, which was easily reached by walking around the bay from the main waterfront. The cave is 17 m wide x 13 m high with a depth of 10 m. There was no sediment within the cave, but soils had formed at the base. The cave was occupied by owls, presumably barn owl *Tyto alba* (Scopoli, 1769), although none were seen, as the floor was littered almost exclusively with rat remains, almost certainly *Rattus norvegicus* (Berkenhaut, 1769). A sloughed skin of a snake was also found, but no skeletal material other than recent was present.

Fossil potential of Mayotte caves:

Extremely poor. Only one sea cave was found on Mayotte and no others were known to the local community. Mayotte is the most weathered of the Comoros Islands, and it seems likely that any caves would have collapsed, eroded away or been in-filled with sediment long ago.

Conclusion

In theory the Comoros archipelago appeared to provide great potential for the preservation of fossil material, but in practice proved totally unproductive. All caves surveyed were basaltic as the Comoros lack limestone deposits, which is unfortunate as the caves and sinkholes that have proved to be palaeontologically productive on other western Indian Ocean islands, e.g. the Mascarenes (Cheke & Hume 2008) have been limestone ones. However, only cave sites were surveyed on this trip, so there is still a chance that a marsh or sand dune locality may hold some remains of the original vertebrate fauna.

Unfortunately, the Comoros Islands are subject to intense human pressure, primarily due to severe poverty and high population growth, with deforestation being the most critical factor; the associated soil erosion has noticeably infilled caves on

Anjouan. It is hoped that further longer term investigation can take place, but the present politically unstable nature of the islands lowers the likelihood of this in the foreseeable future.

Acknowledgements

We thank Action Comores and, in particular, Hugh Doulton for assistance in the field on Anjouan.

JPH is deeply indebted to the Trustees of the Special Funds, Natural History Museum, London, for making his travel to the Comoros possible, and for their patience while he was overcoming the delays and uncertainties of safe travel to the islands.

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A further note on *Hypolimnas bolina* in Seychelles

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The great eggfly butterfly, *Hypolimnas bolina* (L.) is widely distributed throughout the Oriental region (Corbet & Pendlebury, 1992), with odd Afrotropical records from Kenya, Ethiopia (Larsen, 1996), Mauritius (Williams, 2007) and Madagascar (Paulian, 1956). In Seychelles, a single male was seen on Alphonse Island on the 1 April 2007 (Betts, 2009). A additional unverified Seychelles recorded was made by Hill, *et al.* (2002) on Marianne Island.

During a recent visit to the University Museum of Zoology Cambridge, UK, a further female *H. bolina* specimen from Mahé was discovered (Fig. 1-2). The specimen was collected on Mahé on 16 May 1914 by H.P. Thomasset and is clearly the subspecies *jacintha* (Drury). The specimen has a wingspan of 82mm.

Hypolimnas bolina is a well known migrant species and it appears that vagrant specimens or ephemeral populations are occasionally found in Seychelles.

Acknowledgements

I would like to thank Mr. R. Stebbings from the University Museum of Zoology, Cambridge for allowing me access to the collection.



Fig. 1. Female *Hypolimnas bolina jacintha* upperside from Mahé, Seychelles, collected 16 May 1914.



Fig. 2. Female *Hypolimnas bolina jacintha* underside from Mahé, Seychelles, collected 16 May 1914.

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Eradication of the invasive common myna, *Acridotheres tristis*, from Fregate Island, Seychelles

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Abstract: The common myna (*Acridotheres tristis* Linnaeus, 1766) is considered a serious threat to the endemic and endangered Seychelles magpie robin (*Copsychus sechellarum* Newton, 1865) on Fregate Island and the complete eradication of mynas was seen as a priority in view of the importance of Fregate for the continued survival of the Seychelles magpie robin. These birds have never been completely eradicated, largely due to the failure to continue with eradication efforts after reduction of the population. A combination of new methods, as well as methods that were at least partially successful in the past, were implemented to ensure complete eradication. This was achieved in February 2011 and took approximately eight months of regular effort from June 2010. Capture methods were adapted and changed for individual birds that had, or that developed an aversion to a particular method. Cage trapping using a commercially available trap was by far the most effective method of capture. A total of 745 birds were destroyed, along with 42 eggs.

Keywords: threat, magpie robin, complete eradication, pest management

Introduction

The common myna *Acridotheres tristis* Linnaeus, 1766 was introduced to Mahé from Mauritius and has spread through the granitic islands of the Seychelles where it is common on the majority of the larger islands. They are common around human habitation where they congregate in large flocks at dusk (Skerrett *et al.* 2001). On Fregate they also gathered in large numbers at the dump site during the early morning hours when food waste was dumped. They are omnivorous and forage in a number of different habitats where they competed with the Seychelles magpie robin for food.

Biological invasion by non-native species is recognized as one of the major threats to native species and ecosystems and such invasions are contributing to biodiversity decline (Holzapfel *et al.* 2006). In 2000 The World Conservation Union declared the common myna as one of the 100 worst invasive alien species (Lowe *et al.* 2000) and they posed a threat to indigenous biodiversity on Fregate, through competition for food and nesting resources (Peacock *et al.* 2007; Millet *et al.* 2005). On Fregate they were observed making use of tree hollows, coconut palms (*Cocos nucifera*), eaves of roofs and nesting boxes of Seychelles magpie robin for nesting sites. As a member of the Convention on Biological Diversity, the Seychelles has a responsibility to “prevent the introduction of, control, or eradicate those alien species which threaten ecosystems, habitats or species” (United Nations 1992) and the complete eradication of this bird from the island was seen as a priority.

Fregate is, at present, the most important island in the Seychelles for the

continued survival of the Seychelles magpie robin and any threats to their survival need to be eliminated. Between the 1950's and 1990's the entire population was restricted to Fregate and at times came very close to extinction (Bristol *et al.* 2005). These birds are present on five granitic islands with Fregate hosting at least 92 birds out of a total population of 209 individuals (Derand 2010). Whilst the status of the bird has been downlisted from Critically Endangered to Endangered it is still one of the worlds' rarest birds and requires conservation management (Birdlife International 2010); including the removal of alien species that threaten their survival. All introduced mammalian predators have been eradicated from Fregate. Cats and rats were eradicated in 1977 and 2000 respectively (Henriette Payet 2007). Common mynas were also seen as being a threat to the Endangered Seychelles white eye (*Zosterops modestus* Newton, 1867) population on Fregate (Henriette Payet 2007). They have also been observed predated on the eggs and chicks of the Critically Endangered Seychelles black paradise flycatcher on Denis Island (*Terpsiphone corvina* Newton, 1867) (Feare 2010b) and there is the possibility that this behaviour may occur with other native species. Possible future introductions of native and endemic species will only be successful if threats to their survival are eliminated. Extensive habitat alteration and degradation of the island as well as the availability of a constant food supply has meant that the common myna was able to thrive on the island.

Study area

The Seychelles islands lie approximately 1500km off the East coast of Africa. Fregate lies at 04°35'19''S and 55°56'55''E and is the most isolated of all the Seychelles granitic islands (Skerrett & Skerrett 1990). It lies 55km from Mahe and is 219 hectares in size.

The Seychelles islands were part of the Gondwanaland supercontinent, with Fregate composed of granite overlying oceanic basalt. Deposits on the plateau are associated with guano; forming phosphate cemented sandstones and phosphatized granite. The low-lying areas were previously marshy and characterized by sediments of fine clay and quartz (Braithwaite 1984). It is a privately owned island that has the 125m high Mont Signal as its highest point. Although Fregate was once covered in lush vegetation, exotic species now dominate. It is used as a tourism destination and has a small hotel that caters to a low numbers of tourists at any time.

Rainfall records on the island are inconsistent and unreliable. Records from 1972–2001 from the Seychelles capital, Victoria, on Mahe, give an average annual rainfall of 2319.8mm (Seychelles National Meteorological Services, undated).

Methods

Previous attempts to eradicate the common myna from Fregate, using a police marksman to shoot the birds and nest box trapping, were unsuccessful as the lack of constant effort permitted the population to recover (Millet *et al.* 2005). Previous attempts, as well as information from eradication efforts on other Seychelles islands were taken into account in determining the best methods for eradication. Decoy traps were found to be successful on Denis Island (Feare 2010a) and it was decided that cage

trapping would be the most effective method; supplemented by nest trapping, shooting and elimination of eggs and pulli from known nests. A combination of methods ensured that individuals that developed trap aversion were still eliminated. Chemical control was not considered due to its non-selectivity and the possibility of affecting the Seychelles magpie robin population. Areas of high myna concentrations were targeted by cage trapping until these cages no longer trapped any birds for a period of two to three weeks. Individual birds or pairs were then targeted using different methods until all individuals were eradicated.

Mynas were heavily concentrated in areas of human habitation and usage. The highest concentrations of these birds were the island dumpsite, where food waste as well as other waste is disposed of and a tortoise pen where juvenile tortoises are raised before release onto the island. Other areas where successful cage trapping occurred included cultivated fields, manicured lawns and the commercial airstrip where these birds foraged. The initial phase of the programme used only cage traps in these areas of high concentration. Only once the population had been substantially reduced and the cages were no longer effective, were supplementary methods employed.

Shooting

Shooting as a primary method of eradication was determined not to be a viable option due to the size of the myna population and the high concentration of mynas in particular areas. Any shooting attempts in these areas would likely have lead to gun shyness in a very short period of time. Some of the population was also likely to be gun shy as a result of shooting in the past. This method was used only as the opportunity presented itself and was only used on individuals, not on pairs or groups. A Gamo CF-30 air-rifle was used with 5, 5 (22) calibre pellets.

Nest trapping (Fig. 1)

Nesting boxes have been provided for the Seychelles magpie robin as a conservation measure due to the limited availability of naturally occurring nesting sites. These nesting boxes were largely utilized by the mynas as nesting sites. Nylon nooses were placed in boxes known to be occupied by a pair of mynas. Three nooses were placed over the entrance holes of the nesting boxes, hanging from above. They overlapped one another to ensure successful capture. Two or three further nooses were placed in the central section of the box. The diameter of the nooses was approximately 5cm and they were held in place within the box by staples. This method was only used at one site after other methods failed to capture these particular birds.

Cage trapping (Fig. 2)

MiniMyna traps were used. These traps are manufactured by Myna Magnet Australia Pty Ltd. The trap consists of two parts, namely the holding cage and the feeding cage, in which the bait is placed. The feeding cage has two walk-ins that allow the birds to enter this section but not to leave due to the funnel shape of the walk-ins. A fuzzle valve leading from the feeding cage to the holding cage allows the mynas to enter the holding cage. The valve has springs attached that allow the bird to fly upwards but

Fig. 1. Nesting box showing nylon noose placement



not back down through the valve. The birds' only option once they finish feeding on the bait provided is to fly through the fuzzle valve and into the holding cage. These traps are live traps allowing for the release of any species unintentionally captured by this method. Cages with trapped mynas were placed in a waterproof, non-permeable bag and the birds were humanely euthanized with carbon monoxide from a petrol engine by means of a pipe attached to the exhaust pipe of the engine on one end and the other end placed in the bag.

Cages were baited and left open for approximately a week during the initial phase of the programme to allow the mynas to become habituated to the traps. It was determined through experimentation that cages placed within close proximity to one another (between one to two metres apart) were most effective at catching birds. Caller birds were kept in cages to attract other mynas to the cages. These birds were left overnight to attract mynas the following morning. They were watered and fed to prevent stress. It was found to be preferable to keep two caller birds in a cage rather than one as the mynas appeared less stressed this way.

The number of cages used at particular sites was determined by the concentration of mynas at the particular trapping site. The dumping site on the island had by far the highest concentration of mynas and nine cages were used at this site. This site attracted large numbers of mynas to readily and regularly available food. Food waste is dumped at this site twice a day; once in the morning and once late in the afternoon. Myna visits to this site coincided with dumping times and the setting up of the cages was timed

Fig. 2. MiniMyna trap showing feeding cage on left and holding cage on right.



to coincide with the dumping of food. During the eradication programme food waste was covered up so as to limit availability of food to the mynas and ensure that the only readily available food to the mynas was that used for bait.

Papaya was used as bait as it is readily available to the mynas on the island and they are often found feeding on wild growing papaya. Dog food was attempted as bait, however this proved to be unsuccessful and no mynas were trapped when this bait was used.

Walk-in trap (Fig. 3)

Aversion to mini-myna traps was inherent, or developed in some individuals and pairs. Individuals that could not be eliminated by nest trapping and shooting, due to their nests being inaccessible, were targeted using a walk-in trap. This trap was larger and more open to lure mynas. It was designed and constructed on the island and consisted of a framework of steel poles 1cm in diameter. The frame was 1,5m X 1,5m

Fig. 3. Walk-in trap



X 0,8m in height. A hinged door was attached to one side that swung up and out from the top of the frame. The entire framework was covered in fine shade cloth ensuring that bait was visible to the birds. The door was balanced on a pole that had a nylon fishing line attached. This fishing line was laid between 30-50 m away from the trap and was held by one person unseen to the mynas. Once a myna had entered the trap the line was pulled, dislodging the pole and causing it to fall closed and trap the bird. Once trapped, the bird was killed using an air rifle. Any non-target species trapped at the same time were released after the myna had been shot to prevent unintentional escape of mynas.

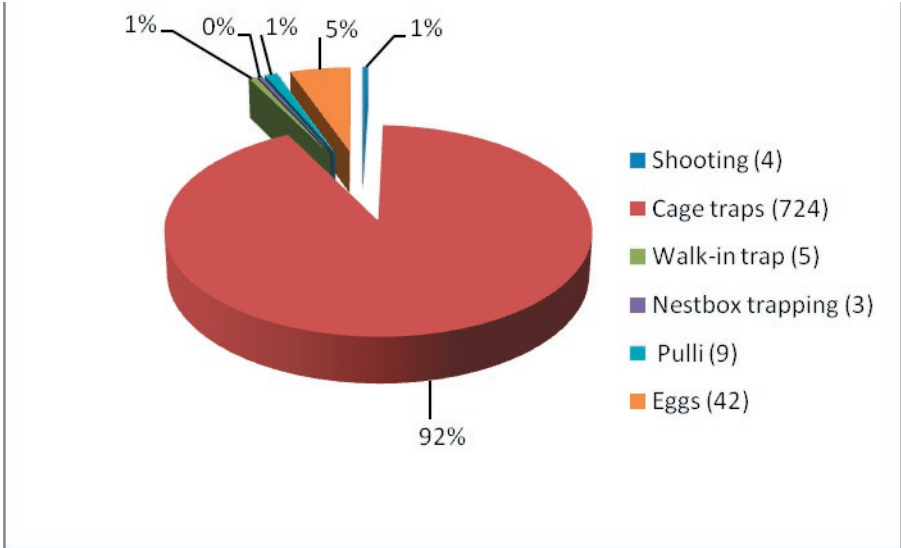
Pulli and egg eradication

Nesting boxes provided for Seychelles magpie robins were regularly used by mynas and during the monitoring of these boxes myna pulli or eggs that were found were destroyed along with nests. Myna nests with eggs and pulli found in the eaves of roofs were also destroyed.

Results

Trapping was started in June 2010 and the last birds were eradicated in mid February 2011. A total of 745 birds of all age classes were destroyed, along with 42 eggs (Figs 4-5).

Fig. 4. Eradication methods and number of birds killed per method



Shooting

Shooting only accounted for four birds, excluding those killed by shooting in the walk-in trap. This method would have accounted for more birds had it been used more regularly and consistently but it was found not to be necessary and the effort required in relation to the number of birds killed made this method inefficient.

Cage Trapping

Trapping was used as the primary method of eradication. 92% of all birds eradicated were as a result of their capture in traps. A total of 724 mynas were caught in these traps. Bycatch of non-target species occurred with the vast majority of these birds being released unharmed. Up to nine mynas were trapped in a single cage. Newly fledged birds would enter the traps in the presence of their parents even when their parents would not do so.

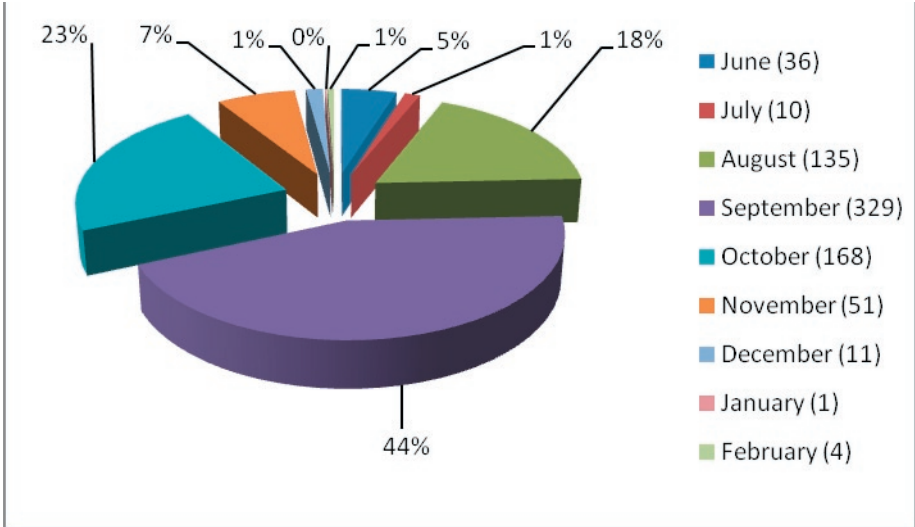
Walk-in trap

This method accounted for five birds and was only implemented after an aversion to cage trapping had developed. Three individuals were caught at the dump site and two on the airstrip.

Nest box trapping

One individual was caught within three hours of setting these nooses. A pair of was caught in the same nesting box the following day. This method would probably have accounted for more mynas had it been used more regularly.

Fig. 5. Monthly eradication figures



Pulli and egg eradication

This method was used during regular monitoring of Seychelles magpie robin nesting boxes. It proved an effective way of destroying known myna nesting sites. During the initial phase of the programme all mynas nests were removed from the nesting boxes. At the latter stages a nest was left in the nesting box to ensure a return to the nesting box by the resident myna pair and nooses were placed in the nesting box.

Bycatch (Table 1)

Non-target species were caught in all areas where cages and the walk-in trap were set, with the majority being caught at the dump site, where these species also fed on food waste. The majority of these individuals were released unharmed from the cage traps and all individuals were released unharmed from the walk-in trap. Four bird species were unintentionally caught, three of which were alien species.

Species unintentionally trapped were Madagascar turtle dove (*Nesoenas picturata* Temminck, 1813), barred ground dove (*Geopelia striata* Linnaeus, 1766) Madagascar fody (*Foudia madagascariensis* Linnaeus, 1766) and the indigenous common moorhen (*Gallinula chloropus* Linnaeus, 1768). Terrestrial hermit crabs of the genus *Coenobita* were trapped in the cages placed on the airstrip on the side closest to the beach. Mynas would not enter cages that had these crabs in them, regardless of the number of crabs in the cages. Cages set on the side of the airstrip furthest from the beach that did not trap crabs, were successful in the trapping of mynas.

Madagascar turtle doves are found on the island in high concentrations and most of those found dead in the traps had their heads caught between the bars of the cage. The majority of Madagascar fodies were able to find their way out of the trap once

Table 1. Bycatch

Method	Species	Number caught	Number dead
Cage trapping	Common moorhen	10	0
	Madagascar turtle dove	77	11
	Barred ground dove	14	1
	Madagascar fody	1	0
	Terrestrial hermit crabs	239	0
Walk-in trap	Madagascar turtle dove	9	0

they had entered and fed on the bait, with only one that became trapped and was unable to escape.

Discussion

Personal observations and anecdotal evidence would indicate that the eradication of the common myna has resulted in a noticeable increase in the number of Seychelles magpie robins that have fledged, as well as an increase in the use of nesting boxes by Seychelles magpie robin. In areas where there were previously high concentrations of mynas, there has been a dispersal of Seychelles magpie robins into these areas. Further monitoring of the magpie robin population will determine to what extent the eradication of the myna has benefitted this species and to verify observations.

After previous eradication attempts the myna population was allowed to grow to substantial numbers. According to Millet *et al.* (2005) the population estimate of mynas on Fregate in November 2002 was 8 individuals, although they do concede that population numbers are extremely difficult to estimate. Figures from 2011 show a substantial increase from 2002 and it is possible that there was some reinvasion from other islands during this period. Personal communications with long term residents of the island indicate that the population had indeed expanded enormously over the last few years. Traps are avoided by mynas if they have previously managed to escape, indicating a degree of learned response. Different capture methods ensure that this learned response is countered. The continuous and regular setting of traps and targeting of these birds ensured that eradication was successful. These birds must not be given an opportunity to increase in numbers once they have been reduced.

Fregate experienced unusually low rainfall during the time that the programme was implemented and it is possible that a shortage of other readily available food encouraged the birds to enter the traps for easily available food. Birds that were habituated to the presence of humans enter the traps readily and were not dissuaded from entering the traps even when they observed the setting up and removal of traps. The use of caller birds appears to increase the success of capture, particularly in those areas where mynas are not as habituated to the presence of humans. This correlates with data from Denis Island (Feare 2010a). The use of caller birds only, without the provision

of bait was not attempted on Fregate. Mynas readily accepted bait that they are familiar with, whilst unfamiliar bait proved unsuccessful.

The common myna specializes in the invasion of woodland, especially those areas modified by the activities of man (Tidemann undated). On Fregate, all mynas were trapped in these modified habitats, with very few birds being found in areas of native woodland. Native woodland had one of the lowest densities of mynas during weekly bird counts over all habitat types found on the island. The vegetation of Fregate has been extensively altered by the activities of man and the majority of the island is covered in alien species. Along with a regular food supply, this is conducive to future reinvasion. Habitat restoration may be a factor in reducing reinvasion and reestablishment of a population and the disposal of food waste in a different manner may help reduce future invasions of this species. The fact that these birds do not have a high rate of mobility means they are slow to spread (Tidemann 2005) and reinvasions may be controlled before the population increases substantially.

It is important to adhere to guidelines to ensure the successful eradication of this species. These guidelines include proper planning, commitment to complete, putting the entire population of the species at risk, removing them faster than they can reproduce and preventing reinvasions (Veitch & Clout 2002). Failure to completely eradicate the species in the past was as a result of not adhering to the above guidelines.

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I also thank Julie Gane, Conservation Manager of Fregate Island Private, for the use of Seychelles magpie robin nesting box data as well as for the maintenance of the myna eradication database.

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Conservation of the Seychelles sheath-tailed bat *Coleura seychellensis* from 1997-2011 and future prospects

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Abstract: The Critically Endangered Seychelles sheath-tailed bat *Coleura seychellensis* has been the subject of conservation activity on Silhouette Island since 1997, in addition research into its status has been carried out on Mahé island. The species was more abundant in the past and many known roosts have been abandoned. The causes of decline have been speculated to include disturbance and predation but studies of the roosts suggest that habitat change may be the most significant factor. The species occupies small caves in boulder fields in lowland woodland which has been extensively invaded by introduced plants. These plants support reduced numbers of insects, especially Coleoptera. Lepidoptera and Coleoptera dominate the diet with a strong preference for the latter before and during the breeding season. Habitat management on Silhouette has removed alien plants from around the roosts and improved foraging conditions for the bat resulting in an increase in breeding activity. The population at La Passe on Silhouette has increased from 14-25 individuals in the 1990s to 40 in 2009. In 2010 this colony fragmented with 18-20 individuals leaving to start a second colony at Anse Lascars. The forced closure of the conservation project in March 2011 means that all conservation action for the species has ceased. In the absence of Seychelles government commitment to support conservation of this Critically Endangered species its future prospects do not look promising.

Introduction

Of the different vertebrates groups, bats seem to be particularly vulnerable to extinction, poorly studied and rarely managed (Micklburg et al. 2002). In recent times one species is known to have become extinct; the Christmas Island pipistrelle *Pipistrellus murrayi* (Lumsden et al. 2009). One of the most threatened species is the Seychelles sheath-tailed bat *Coleura seychellensis*. This species is categorised as Critically Endangered primarily on the basis of its small population size (Gerlach et al. 2008).

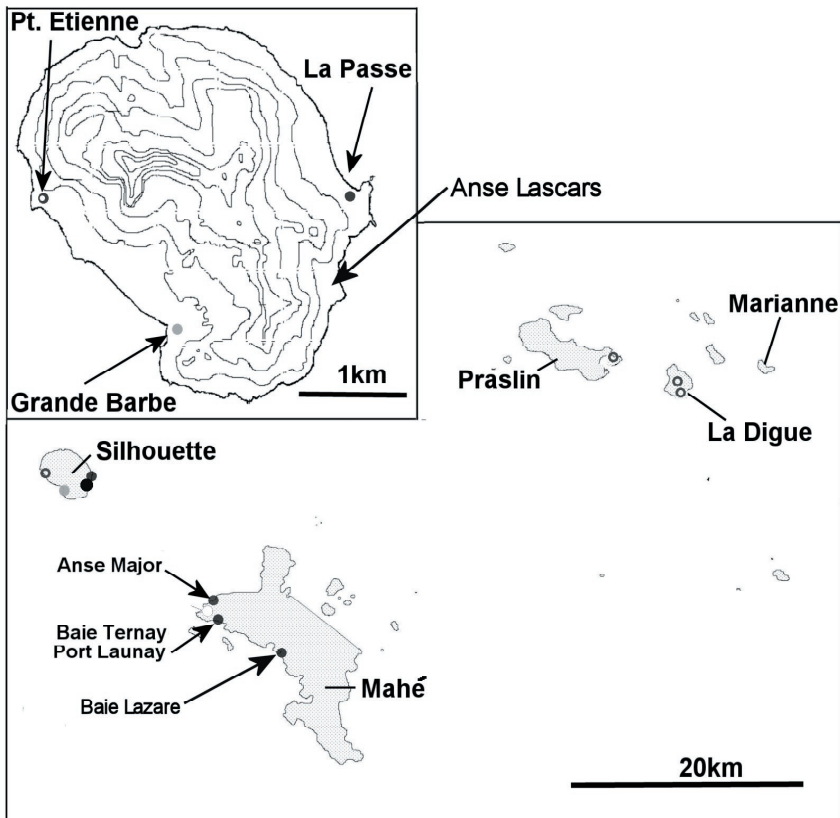
The Seychelles sheath-tailed bat was described in 1868 (Peters 1868) but has only been the subject of significant research in the past 15 years (Burgess & Lee 2004; Gerlach 2004, 2010a, 2010b; Joubert 2004; Rocamora & Joubert 2004; Bambini et al. 2006; Gerlach & Taylor 2006). The 1868 record noted that roost sites were noted to have north-facing entrances screened by palm leaves (Wright 1868). There were no subsequent records until one was shot in 1908 in an attempt to locate parasites (Scott 1914). Research in 1973-1980 located 5 roost sites (2 occupied) with low numbers of roosting bats (1-6 in most roosts) (Nicoll & Suttie 1982). The roost on Silhouette has been monitored by the Nature Protection Trust of Seychelles since 1997 (Gerlach 2004).

The causes of the decline in this species are not known, human disturbance,

predation by barn owls and habitat destruction have been suggested (Nicoll & Suttie 1982; Bambini et al. 2006; Gerlach 2004). The existing Silhouette roost is secure from human disturbance but the invasive Kudzu vine *Pueraria phaseoloides* has threatened to smother the entrance at times (Gerlach & Taylor 2004).

The Seychelles sheath-tailed bat is restricted to the island of Mahé and Silhouette (Fig. 1). On Mahé it is restricted to three roosts containing some 37 bats: Port Launay - Baie Ternay (27 bats), Baie Lazare (8) and Anse Major (1-2 individuals) (Bambini 2008; P. Senior pers. comm.; pers. obs.). On Silhouette three roost sites have been recorded as being active in the past 15 years: Grande Barbe (abandoned in about 2004), La Passe varying from 18-40 individuals and Anse Lascars numbering 18-22. The Silhouette roosts have been the subject of research, monitoring and management by Nature Protection Trust of Seychelles since 1997. The activities undertaken by NPTS for this species are summarised below.

Fig. 1. Granitic islands of Seychelles showing localities mentioned in the text. Occupied roosts are marked with filled circles, historical roosts with open circles. Occasional roosts are marked with shaded circles. Inset – Silhouette Island with 100 m contours shown.



Research

Foraging activity

Research into the Silhouette population has been published in full (Gerlach 2009). This covered the distribution and character of foraging habitat, diet, prey availability, behaviour within the roost, breeding season, reproductive rate and juvenile growth. In terms of conservation management the most important research findings were that foraging ranges changed seasonally in response to prevailing winds and that foraging activity correlated with beetle numbers, which in turn related to management practices (Gerlach 2009). Foraging was only recorded in open areas, in forest clearings or over exposed rocky slopes.

Monitoring

The La Passe roost on Silhouette Island has been monitored since 1997. Installation of roost CCTV in 2006 (Fig. 2) has allowed frequent and accurate counts. Roosts on the west coast have been visited at least once a year since 2005 (Grande Barbe in March/April and December every year and Pointe Etienne in March/April) and searched for signs of recent occupancy - the presence of bats or of recent guano. Guano was categorized as fresh (not completely dry), recent (deposited since the previous visit) or old. No bats have been found in these roosts although occasional small quantities of fresh guano have been located, consequently population estimation is only possible for the La Passe roost. The Anse Lascars roost was formed in 2010 and searches to locate the roost were made in that year. Searches were made in boulder fields and attempts were made to track the movement of bats in the area using automated bat detectors (Anabat II system and SongMeter), these were placed in clearings in woodland or on rocks overlooking the canopy or potential flyways. The bat detectors were set to record between the hours of 18:00 and 06:00. The SongMeter was coupled with an ultrasonic microphone on a 50m extension cable allowing the microphone to be positioned in the canopy.

Fig. 2. CCTV in La Passe roost B

a) positioning of the monitoring camera



b) view from the camera



The main roost on Silhouette is the La Passe roost system (Fig. 3-4). Permanent occupation was found in cave B, with daily use of cave A by some bats. Evidence of occasional use (small quantities of fresh guano but no bats) was found at one site at La Passe (roost D) and old guano found in roosts C and E. An abandoned roost was found at Pointe Etienne (Fig. 4), no roosts could be found at Anse Mondon.

Fig. 3. La Passe roost system. A and B are occupied roosts, D used on at least one occasion in the recent past. C and E are abandoned.

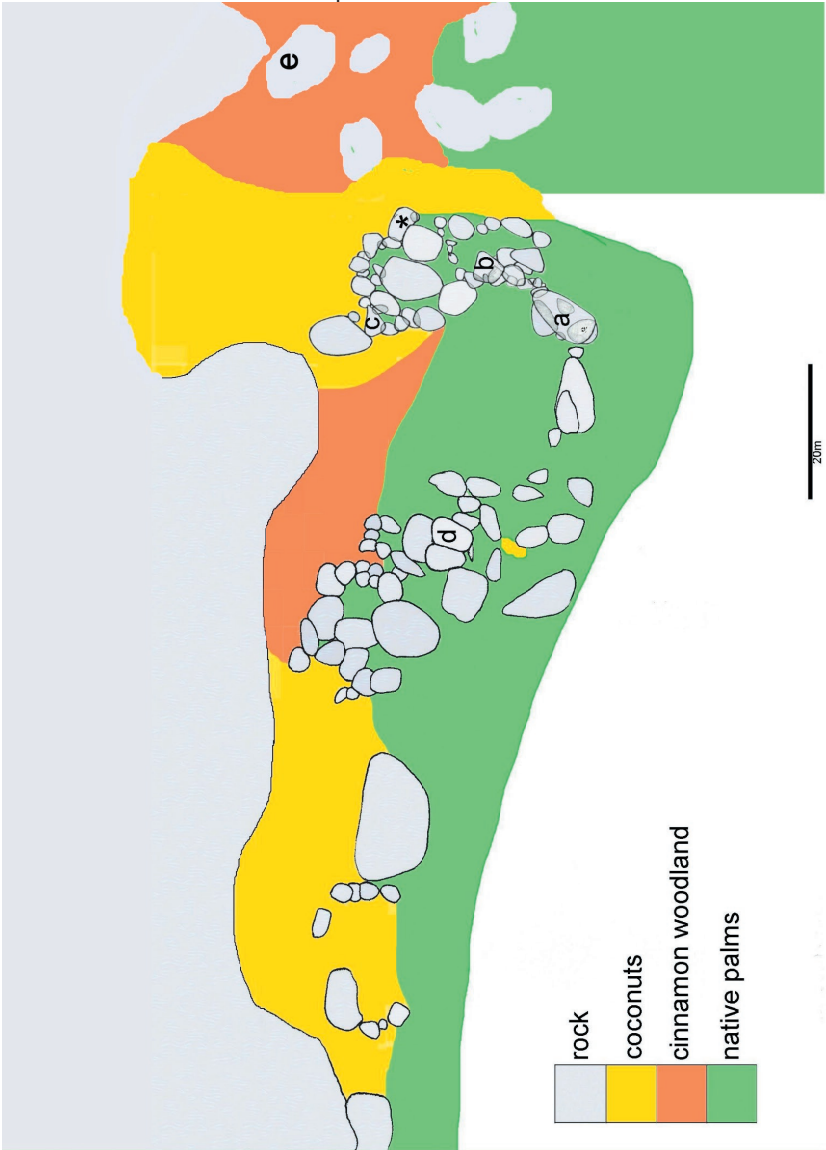
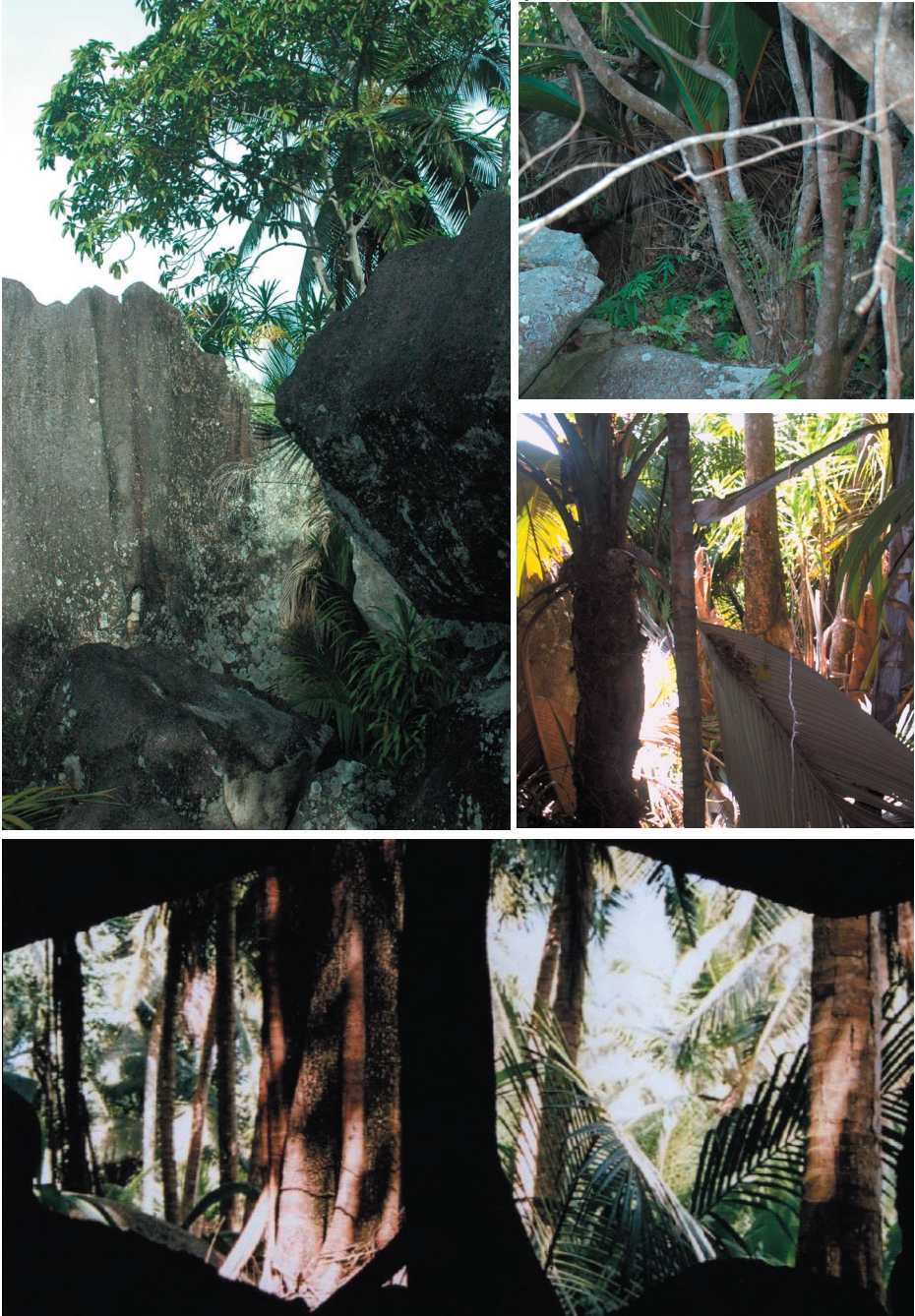


Fig. 4. Views of roosts - clockwise: B, E (entrance), D (view from entrance), Pte Etienne roost (view from entrance; photo : M. Taylor)



Since 2001 the La Passe population has grown significantly (Fig. 5). A maximum of 40 bats was reached in 2009. In March 2010 12 bats left this population and were located at Anse Lascars. A further 6 moved to Anse Lascars in June (Fig. 6). From March 2010 to March 2011 the number of bats at La Passe fluctuated between 18 and 22, suggesting regular movement of some individuals between the La Passe and Anse Lascars roosts.

Fig. 5. Population change in the La Passe roost. Data are grouped into quarters ('Q').

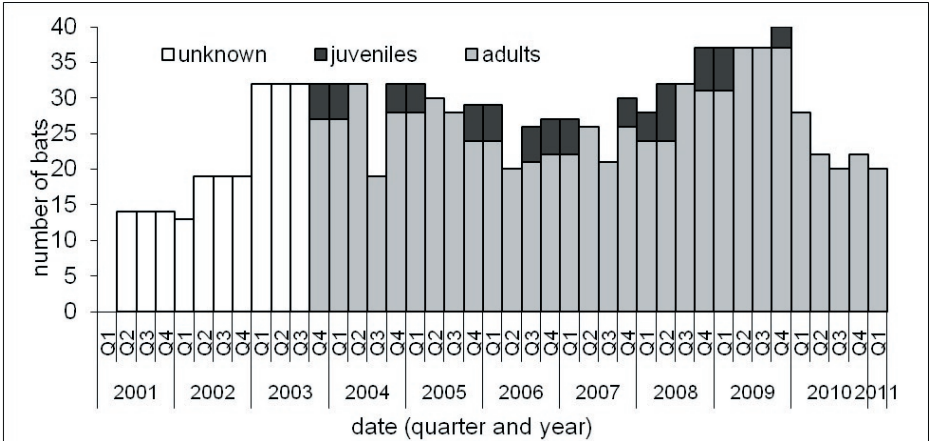


Fig. 6. Bat activity areas on the east coast of Silhouette.
a) Anse Lascars foraging area b) Top – La Passe, bottom – Anse Lascars



At Grande Barbe at least one bat was present between 2006 and 2008 but was not recorded after that date. This probably marks the extinction of that population. From the size of the roost (Fig. 7a) it is probable that a large population used to occur in the area. Habitat degradation (Fig. 7b) is the most likely cause of extinction.

Management

Conservation action covered roost protection and habitat management. Threats to the roost were identified as smoke from fires in the La Passe settlement, rubbish dumping, increases in alien mammal populations, insecticide use and invasive creepers. Direct human disturbance to the roosts is not a significant threat at present (although there are anecdotal reports of deliberate disturbance in the past in some of the abandoned roosts by people knocking bats off the roost ceilings with sticks – Matyot 1995).

Smoke

Until 1998 a copra dryer was in operation 300 m from the roost, during the south-east trade winds season smoke from the dryer was blown directly into the roost throughout the hours of daylight for 5-6 days of the week in the south-east trade winds season. In 1998 an agreement was reached with the island management that no fires would be lit in the vicinity of the roost and since then population increase was recorded in the roost. The creation of a construction workers' camp at the site of the old copra dryer in 2005 (and to the present day) means that a wood cooking fire produces smoke which reaches the roost at times. This was generally at a low level although significant smoke pollution did occur at times. The chemical composition of this smoke is also

Fig. 7. Grande Barbe roost.

7a) roost site

7b) surrounding habitat dominated by coconuts



a cause for concern as the wood being burnt was off-cuts of treated timber from the carpentry workshop.

Rubbish dumping

Rubbish dumping within 250m of the roost started in 2005 when food waste from the hotel labourers' camp was dumped in pits (Fig. 8a). This practice continued until 2007 and resulted in an increase in rats and Indian mynas in the area. Associated with this was a notable increase in cat activity (see below). Since 2007 food waste dumping was replaced by daily dumping of garden waste and household rubbish within the foraging area of the bats (Fig. 8b). Although this practice was reported to the Seychelles Ministry of Environment (NPTS 2007-11) no controls have been put in place.

Alien mammals

As noted above, rat and cat activity increased in the foraging areas used by the bats since 2005. In 2006 the CCTV camera showed high levels of agitation in the roost. No direct cause could be identified but investigation found rat foot-prints in the roost. In October 2006 the roost was completely abandoned but the bats returned in the following month. Rats in the roost may have been a source of direct disturbance or, more significantly, may have attracted cats. From January 2007 three poison bait stations were positioned in the entrance to the roost. These were maintained until March 2008 when it was concluded that the continued high rate of bait consumption could be attributed to snails rather than by rats. No further evidence of rat activity was observed subsequently.

Fig. 8. Rubbish dumping 9a) food waste dumping in 2005, 9b) dumping in 2010 in the National Park



Dog hair was found in roost D in 2006 and a stray dog heard in the vicinity throughout that year. Stray dogs were removed from the island and all domestic dogs neutered in 2007, this appears to have been effective as no stray dogs have been located subsequently. By 2010 no dogs were present on the island.

Predation by barn owls *Tyto alba* has been suggested to be a threat to the sheath-tailed bat (Nicoll & Suttie 1982; Bambini et al 2006). However, this is purely speculative and no data has been presented in support of the suggestion. No evidence of interaction between the two species was found on Silhouette.

Insecticides

Use of DDT for insect control in the mid-20th century may have had some impact but there is no evidence to allow evaluation. In recent years there has been an increase in the application of insecticides applied by fogging around human habitations. On Silhouette this has occurred within 200m of the La Passe roost and insecticide fog was observed drifting up to the roost site in February 2007 (Fig. 9). Such fogging practices have occurred at 3-6 month intervals since early 2006 to provide short-term control of mosquitoes. In March 2007 it was agreed that insecticide use would be restricted to buildings in the main settlement area, at least 300m from the roost and outside foraging areas. Enforcement of this has required continued monitoring as staff changes mean that these regulations are not always adhered to.

Fig. 9. Insecticide fogging



Invasive creepers

In 1997 the La Passe roost was threatened by the proximity of the alien Kudzu vine *Pueraria phaesoloides* which was starting to cover the entrance and change the ecological conditions of the roost. The creepers nearest the roost were cut back in July 2001 and in 2004. The plant seemed to have been eliminated from the area until 2009 when some shoots from underground roots was found and removed. *P. phaesoloides* is restricted to an area of 0.5 hectares on Silhouette (Fig. 10) and was managed by removal of seedling outside of this area. In addition to removal of this plant other invasive creepers (*Passiflora foetida*) were removed from the roost entrance and invasive trees removed selectively. The trees were removed by pruning or by ring-barking so as to cause slow habitat improvement and avoid rapid changes to the microclimate or appearance of the roost areas. Coconut seedlings were removed regularly and coconut leaves obscuring potential flyways removed.

Fig. 10. *Pueraria phaesoloides* invasion



Fig. 11. Habitat management at La Passe
original



2004



2006



Habitat management

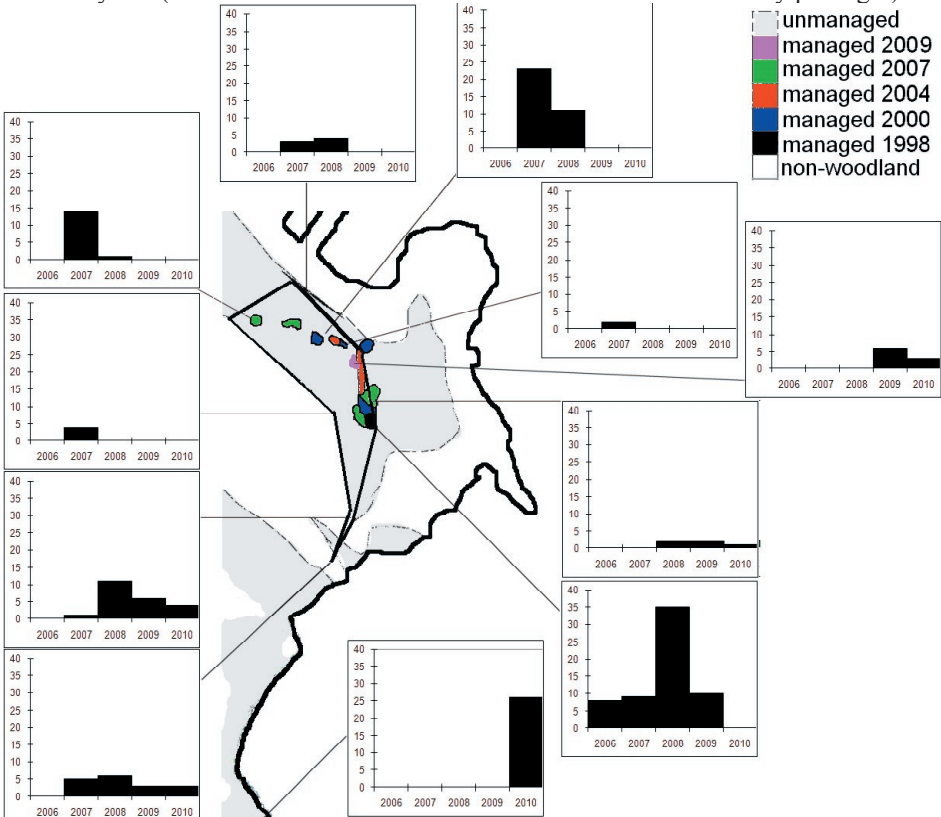
Habitat management was carried out in the foraging areas. Since 1997 *Cinnamomum verum* trees have been selectively removed in these areas to create small clearings. In these clearings existing native plants have been encouraged to grow or have been planted (Fig. 11). This management created a mosaic of un-managed areas, cleared and planted areas of varying ages and closed canopy management areas of varying ages.

Trees planted include fast growing indigenous species (*Ficus reflexa*, *Morinda citrifolia* and *Ochrosia oppositifolia*), indigenous lowland forest trees (*Carissa spinarum*, *Heritiera littoralis* and *Intsia bijuga*) and threatened endemics (*Grisollea thomasseti*, *Mimusops sechellana*, *Northea hornei*, *Rothmannia annae* and *Tarrena seychellensis*) and scarce endemics (*Vershaaffeltia splendida*). Endemic herbaceous plants have also been established (*Allophyllus seychellensis* and *Gynura seychellensis*). Habitat management was carried out by NPTS (1997-2011) with occasional assistance from volunteers, the Sussex University field course (2000-2010) and Labriz Hotel (2008-2010). This management was highly successful in increasing bat foraging activity in management areas (Fig. 12).

Discussion

At present there is no legal protection of bats in Seychelles. In 2009 it was proposed that most of Silhouette should be declared a National Park. With the support

Fig. 12. Habitat management areas at La Passe showing the woodland areas and the dates of the start of management. Graphs show bat activity levels in different years (measured as mean number of seconds of recorded activity per night).



of international conservation organisations NPTS successfully lobbied the Ministry of Environment to have the proposed area extended to include all areas occupied by the sheath-tailed bat. In 2010 the Silhouette National Park was designated, providing legal protection for all of the Silhouette bat areas.

The research and management carried out by NPTS since 1997 has demonstrated that population recovery can be achieved for the Seychelles sheath-tailed bat. This requires effective protection of roosts and management of roosting and foraging habitat. Most crucially beetle-rich foraging areas need to be restored through the control of invasive plants. This is best achieved by restoring lowland areas to mixed woodland rich in the native plants *Phoenicophorium borsigianum*, *Nephrosperma vanhouetteana*, *Pandanus balfouri*, *Mimusops sechellarum*, *Intsia bijuga*, *Calophyllum inophyllum* and *Premna serratifolia*. Lowland marshes may also be important in some areas although lowland woodland is more significant (Gerlach & Taylor 2006).

Substantial investment in bat research and management by NPTS (Table 1) has enabled the Silhouette population to grow from 18 individuals to 40 and for the species to start to recolonise some of its historical range on the island. The eviction of NPTS from Silhouette in March 2011 puts these achievements at jeopardy. With the cessation of all conservation activity on the island the habitat management has ceased and it is inevitable that invasive plants will start to regain their dominance in the area, reversing the habitat quality improvements. The bats are no longer being monitored and no-one will ensure that pesticides are not used within the foraging areas, or that rats are controlled if populations increase in association with the ongoing rubbish dumping within the National Park.

Conservation prospects on Mahé are similarly poor due to the lack of action by the Ministry of Environment. The 14 years of experience with the Seychelles sheath-tailed bat has shown that reversing the conservation decline of this species is perfectly manageable but cannot be sustained in the absence of a supportive governmental framework. Consequently this species will needlessly remain Critically Endangered with a very real prospect of extinction in the near future.

Table 1. Investment in Seychelles sheath-tailed bat conservation

Item		Expenditure (\$)	Source
Research	entomological equipment	1,200	NPTS
	bat detectors	6,954	CI, SAN
	consumables	28	NPTS
	Time	8,736	NPTS
	Transport	4,721	CI
	GIS	9,450	CI
Monitoring	CCTV systems	3,767	CI, private sponsors
	Time	100,020	NPTS
Management	Labour	1,150	CI, NPTS
	Time	76,800	NPTS
TOTAL		212,826	
		NPTS provision \$182,124	

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Population assessment of the Fregate Island giant tenebrionid beetle *Polposipus herculeanus*

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Abstract: *Polposipus herculeanus* Solier, 1848 is a critically endangered member of the Tenebrionidae and is endemic to a single island of approximately 2 km² in Seychelles. Vegetation changes have occurred on the island over the years and continue to occur, both naturally and as a result of habitat restoration. Vegetation that was considered important habitat for this beetle has changed as a result of a fungal disease that affected the dominant tree species in this habitat. Surveys of the population have occurred previously; prior to rat eradication and shortly thereafter. This assessment was conducted to compare results with these previous assessments to determine whether vegetation changes have had an effect on the population. Comparison of results indicates that the population is stable and that vegetation changes have not necessarily had an adverse effect on the population.

Key words: *Polposipus*, endemic, changes, assessment, stable

Introduction

Polposipus herculeanus Solier, 1848 is a large, flightless tenebrionid beetle that is Critically Endangered - category B1 + 2c (IUCN 2010) and endemic to Fregate Island in the Seychelles islands. There is limited information on its ecology in the wild and disputed claims as to its historical distribution (Marshall 1982). Assessments of the population have been carried out in the past by, amongst others, Lloyd (1971), Lucking & Lucking (1999), Mellor (2002) and Gerlach (1999, 2002). These beetles were found to occur in specific habitat types and to avoid others. Habitat types have changed in size and composition since 2002 as a result of habitat restoration as well as natural vegetation regeneration. Along with vegetation change, it has been over 10 years since the successful eradication of rats from the island (Shah 2001). Brown rats *Rattus norvegicus* colonized Fregate in 1995 and were considered to be predators of these beetles (Parr 1999). Along with rats the common myna *Arcidotheres tristis* was seen as a possible predator of these beetles (Sachse as quoted by Ferguson & Pearce-Kelly 2004). The myna has been successfully eradicated (Canning 2011) and this may have an influence on beetle numbers in the future, although it is too early to determine this as these birds have only recently been eradicated. It would also be difficult to prove this as there is no data to substantiate this claim.

The impact of alien species on native species is well documented and Fregate has not escaped the negative consequences of these introductions. The vegetation of Fregate has been significantly altered by the activities of man, with alien species dominating. The introduction and establishment of alien species has the potential to displace or

exterminate native species and species with small populations and limited range, such as *P. herculeanus* are especially vulnerable (Van Dyke 2003). These alien species have undoubtedly had an impact on the native fauna of Fregate, including *P. herculeanus* and the absence of *P. herculeanus* from large areas of the island is almost certainly largely due to the predominantly unnatural state of the vegetation. *P. herculeanus* has a limited distribution on Fregate, although the potential exists for an expanded distribution into areas of suitable habitat. Areas of suitable habitat are however severely fragmented and isolated from one another. This fragmentation of habitats is a grave threat to species survival (Laurance 2010). The isolation of individuals between habitat types is of concern as it may have negative consequences such as the inability to supplement numbers, decreased gene flow and decreased possibility of recolonization in suitably restored habitats as well as increased chance of mortality during dispersal in poorly connected areas (Bennett & Saunders 2010). The expansion of natural and fragmented habitats is a critical priority in increasing animal assemblages (Bennett & Saunders 2010) and for this reason habitat restoration is an important conservation activity on Fregate. Assessment of the effect that habitat restoration has had on various species has never taken place and the fact that this beetle is restricted to Fregate and is critically endangered makes it imperative that current restoration activity has no negative impact on this species. These beetles are seen as having low powers of dispersal due to their large size and their inability to fly (Ferguson & Pearce-Kelly 2004) and all future restoration needs to ensure that the dispersal of this species into suitable habitat is not in any way restricted.

Despite a limited distribution these beetles have been found to occupy a number of different tree species, both native and non-native. *Pterocarpus indicus*, an introduced species, was used by these beetles. It was considered an important habitat type (Lloyd 1971, Mellor 2002) and *P. herculeanus* was found on this species in relatively high densities (Lloyd 1971). *P. indicus* no longer exists on the island as a result of sandragon wilt with reports of the first death of this tree from 2001 (Boa & Kirkendall 2004) and the last tree dying in approximately 2004 (Goza, pers. comm.). This assessment determined that these beetles are still found in the areas where *P. indicus* occurred although their densities vary significantly between these sites, depending on the size and age of the trees that have replaced *P. indicus*. The area of Au Salon has been allowed to regenerate naturally with little interference and at this site beetles prefer decaying *P. indicus* rather than living trees of other species that have replaced the *P. indicus*. *P. indicus* woodland in the Anse Parc area has been restored and replanted with indigenous species. This assessment included the entire island, covering all habitat types and a comparison of results from previous assessments indicates that the population is stable.

Study area

Fregate Island lies at 04°35'19''S and 55°56'55''E and is a privately owned granitic island of 219 ha lying 55 km East of Mahé (Merton *et al.* 2002). It is a granitic island overlying oceanic basalt. Deposits on the plateau are associated with guano; forming phosphate cemented sandstones and phosphatised granite. The low-lying areas were marshy in the past and characterized by sediments of fine clay and

quartz. (Braithwaite 1984). These marshy areas have since been replaced by cultivated fields, gardens and a marina development. Fregate is largely covered in introduced species, with patches of native woodland that have either persisted or been replanted. Rainfall records on the island are inconsistent and unreliable. Rainfall records from 1972–2001 in Mahé give an average annual rainfall of 2319.8 mm (Seychelles National Meteorological Services, S.a.).

Methods

The assessment was carried out in March 2011 during the wet Northwest monsoon when beetle abundance was previously determined to be at the highest (Lucking & Lucking 1999). The survey assessed only the adult population found on trees and was carried out in the early mornings when beetles tended to be more visible and individuals were not yet sheltering in cracks and crevices. Surveys were not carried out during heavy rain as beetles were less visible and appeared to seek cover under these conditions.

Protocols and methods used by Gerlach in 1999 and 2002 were adapted and used to ensure consistency and a standardized method to allow for comparison of results. The entire island was assessed based on a habitat approach to determine which habitats are important for the cohort. The island was stratified into vegetation types and each vegetation type was determined using maps from Gerlach (2003) and Henriette & Rocamora (2010) and adapted based on vegetation changes that have occurred since these maps were produced. Differentiation of vegetation types is easily determined in the field as there are clear boundaries, largely as a result of the unnatural state of the vegetation of the island. Google Earth was used to produce a map of vegetation types after ground-truthing. In each habitat type 20 trees were randomly selected, marked and inspected on different occasions for the presence or absence of beetles. Trees were marked with plastic marker tape, numbered and their G.P.S. co-ordinates were recorded to ensure the same tree was surveyed on each occasion. The height of the beetles was recorded as well as the species of tree. Trees less than 2 m tall were excluded from the random selection. This was done as Mellor (2002) determined that beetles preferred trees with a larger diameter at breast height. Personal observations also determined that beetles appeared to avoid smaller trees. All visible beetles were marked using a non-toxic over-all multi- purpose correction fluid pen. Beetles were marked on the tree with minimal disturbance. Generally the beetles did not move during or after marking. A single mark of approximately two to three millimetres in diameter was placed randomly on the elytra. Beetles were reached and marked using a 5 m long ladder and by climbing the tree. This mark-resighting was used to obtain a mean of beetles per tree and to determine whether there was a recurring absence or presence of individual beetles on the randomly selected trees. A pilot survey was conducted in all vegetation types to determine the presence or absence of beetles within each stratum. Those strata that were found to contain no beetles were excluded from the survey. In regenerated native woodland, decaying logs (both on the ground and still standing), were included in the survey as beetles were found on these logs in the pilot study. In all other vegetation types only living trees were included in the survey.

Vegetation types

Vegetation types are described based on dominant species and relative homogeneity. They are determined to allow for repeatability of surveys. In the individual descriptions below, only dominant species and those species that were included in the random selection of trees were included. Tree densities were determined per vegetation type by using a belt transect method. Transects of 100 m by two metres were used and all woody species above two metres were included in the survey. At least five transects were included in each vegetation type.

Habitat type 1 - Coconut dominated. Predominantly *Cocos nucifera* with abundant *Anacardium occidentale* and *Cinnamomum verum* and very low densities of *Premna obtusifolia* and *Ficus* spp.

Habitat type 2 - Exotic scrub planted with natives. Dominated by *Chrysobalanus icaco* and *Panicum maximum*. Common indigenous species are *Terminalia catappa*, *Premna* and *Mimusops seychellarum*. Exotic species include *Cinnamomum*, *Manguifera indica* and *Anacardium*.

Habitat type 3 - Mixed woodland. This vegetation type consists of replanted indigenous species such as *Ficus* spp., *Premna* and *Terminalia* and exotic species are dominated by *Manguifera*, *Cinnamomum* and *Paraserinathes falcataria*

Habitat type 4 - *Pisonia* woodland. This vegetation type is a monospecific stand of mature *Pisonia grandis*. It is the smallest vegetation type and the only monospecific stand of *P. grandis* on the island.

Habitat type 5 - Coastal woodland. This area is dominated by replanted indigenous species. It includes *T. catappa*, *Heritiera littoralis*, *Calophyllum inophyllum*, *Hernandia nymphaefolia* and *Ochrosia oppositifolia*

Habitat type 6 - Native regenerated woodland. This area historically consisted of a stand of *Pterocarpus indicus* and has been allowed to regenerate naturally after die off of *P. indicus*. The trees in this vegetation type are still small and consist mostly of indigenous species. This area has not been extensively replanted and the majority of trees have naturally regenerated (Goza pers. comm.). This area is dominated by *Premna* and *Dracaena* spp. and includes *Calophyllum* and *Terminalia*. *Cinnamomum* is the most abundant alien species. This vegetation type has high tree densities due to the fact that the area has not yet progressed to a climax state.

Habitat type 7 - Native planted woodland. As with habitat number 6, this area consisted of a *Pterocarpus indicus* stand and has been replanted with indigenous species after die off of *P. indicus*. Many of the replanted trees were already large when replanted and this habitat is dominated by *Ficus* spp., *Premna* and *Pisonia*.

Habitat type 8 - *Alstonia* dominated mixed exotic woodland. This habitat type dominates the central southern section of the island and extends from inland of the marina almost to Grand Anse. It is dominated by mature *Alstonia macrophylla* and *Cocos nucifera*, interspersed with *Hevea brasiliensis*, *Cinnamomum* and *Anacardium*. Few indigenous species are found in this vegetation type.

Habitat type 9 - Mixed exotic scrub. This vegetation type is dominated by *Chrysobalanus* interspersed with *Anacardium* and *Cinnamomum*. It extends from the plateau into lower-

lying areas. The plateau is sparser than the lower lying areas. Other species include *Mangifera*, *Ficus benghalensis* and *Casuarina equisetifolia*.

Habitat type 10 - Open grassland with natives. This area is dominated by open grassland with sedges. Species that have been planted include *Calophyllum*, *Terminalia*, *Ochrosia* and *Cordia subcordata*. *Cocos* is common in the open areas where indigenous species have not been planted.

Habitat type 11 - Bamboo. This monospecific vegetation type dominates the central section of the island and has outcompeted all other vegetation along the Rivière Bambou.

Habitat type 12 - Coconut plantation. These areas are monospecific stands of *Cocos* and dominate the coastal areas, although they do extend inland.

Habitat type 13 - Glacis. These open, exposed rocky areas are mostly on the plateau and dominated by *Chrysobalanus* and *Panicum maximum*.

Habitat type 14 - *Ficus benghalensis*. This species is found over a wide area of the island. Thick stands occur within *Alstonia* dominated mixed exotic woodland, as well as in coastal areas and around the hotel and villas. Stands are also found on other areas

Figure 1. Habitat types occupied by *Polposipus herculeanus*.

Key: 1. Coconut dominated, 2. Exotic scrub planted with natives, 3. Mixed woodland, 4. *Pisonia* woodland, 5. Coastal woodland, 6. Native regenerated woodland, 7. Native planted woodland, 8. *Alstonia* dominated mixed exotic woodland, 9. Mixed exotic scrub, 10. Open grassland with natives



of the island. It can be considered a separate vegetation type due to the size of area they cover and due to their ability to outcompete other vegetation.

Habitat type 15 - Native planted woodland type 2. This vegetation type occurs in coastal areas and is recently restored. It is found within coconut plantations. Replanted species includes, *Premna*, *Terminalia*, *Calophyllum* and *Ficus* spp.

Results

Of the fifteen primary vegetation types identified, ten were found to contain populations of beetles. Those habitats that did not have beetles were bamboo, coconut plantation, glaxis, native planted woodland type 2 and *Ficus benghalensis*. These habitat types were excluded from the assessment and in the analysis of the data and are considered unsuitable potential habitat. The absence of beetles in coconut plantations and *F. benghalensis* is corroborated by Ferguson & Pearce-Kelly (2004).

The distribution of the population between habitat types was found to be greatly skewed. After data transformation the results from one-way ANOVA indicates that there is a statistically significant difference between choice of habitat type ($F = 3.1814$, $P < 0.05$). Dispersal of beetles between vegetation types was found not to be random and their distribution is clumped which is in agreement with the results of Mellor (2002).

The highest densities of beetles were found in *Pisonia* woodland (habitat type 4) and mature native planted woodland (habitat type 7). Native regenerated woodland (habitat type 6) had one of the lowest densities of beetles. This low density may be explained by the fact that this habitat type is not yet mature after die off of *Pterocarpus*

Figure 2. Comparison of population of *P. herculaneus*. 1999 and 2002 estimates as determined by Gerlach (2003).

Year	Estimate	Upper limit	Lower limit
1999	57,060	66,098	48,022
2002	50,390	53,678	47,102
2011	54,351	67,879	43,511

Figure 3. Surveyed habitat types

Habitat type	Area surveyed in m ²	Tree densities per hectare	Beetle densities per tree
Coconut dominated	191,690.4	1,225	0.475
Exotic scrub planted with natives	41,751.62	700	0.975
Mixed woodland	57,450.98	1,050	1.075
Pisonia woodland	6,293.38	2,800	1.225
Coastal woodland	54,350.72	1,400	0.625
Native regenerated woodland	18,871.54	2,340	0.35
Native planted woodland	6,672.34	1,100	1.3
Alstonia dominated mixed exotic	211,339.92	1,120	0.575
Mixed exotic scrub	119,813.33	1,140	0.75
Open grassland with natives	45,212.71	425	0.3

indicus. Beetles found in this habitat were for the most part found on decaying *P. indicus* logs that were both lying and still standing. The native planted woodland has mature trees and beetles were found on these trees. No beetles were found on the decaying logs of *P. indicus* that are still found in this habitat type.

A population estimate was obtained by determining the means of beetles observed on the 20 trees per vegetation type in conjunction with tree densities over area of habitat. Data obtained indicated a skewed distribution of the population between habitat types. This skewed data was partially as a result of unexpectedly low densities of beetles in regenerated native woodland. Data was transformed using a logarithmic transformation to give an estimate of μ . The result was then multiplied by the number of sampling units to give an estimate of the population.

Population estimate of *Pulposipus herculaneus* on Fregate was determined to be 54,351 with an upper limit of 67,879 and a lower limit of 43,511. No beetles were found in seemingly suitable habitat on the southwestern side of the island and most lower lying areas appeared to have lower densities of beetles which is in agreement with results of Lucking & Lucking (1997). *Pisonia* woodland is an anomaly in this respect, although this may be explained by the protection against the elements afforded by this vegetation type. Further surveys would be needed to explain this.

Discussion

The population of this beetle appears stable when Gerlach's estimates from 1999 and 2002 (Gerlach 2003) are compared with 2011 estimates. The population has increased since the assessment in 2002 after a decrease from the assessment in 1999 and this is probably as a result of a population increase after the eradication of rats.

These beetles appear to choose specific tree species and avoid others; however the reason for this is unclear. They are found on smooth barked trees, such as *Alstonia macrophylla* (corroborated by Mellor 2002) and *Pisonia grandis* that offer few cracks and minimal or no peeling bark for sheltering purposes, as well as on *Manguifera indica*, *Anacardium occidentale* and others that are fissured and flaky and offer much shelter. They avoid *Ficus benghalensis* and *Cocos nucifera* that have similar characteristics to those species that are utilized and some other factor must determine their avoidance of these tree species.

Pisonia woodland was found to have one of the highest densities of beetles. In previous assessments, no mention is made of this. It is unlikely that these beetles have only recently dispersed into this habitat type as it is a mature stand. It is more likely that this habitat was previously overlooked or has been included in other habitat types in previous surveys and not assessed separately, due to its small size and the fact that is situated on the periphery of coastal woodland and mixed woodland. This site is of conservation concern, as not only does it have high densities of adult beetles, but larvae of the beetle have also been found here by Pearce (*pers comm.* 2011). There is also a high density of millipedes (*Seychelleptus seychellarum*) and other invertebrates as well as skinks (*Mabuya wrightii* and *M. sechellensis*) and snakes (*Lamprophis geometricus* and *Lycognathophis sechellensis*). It is also inhabited by Seychelles magpie robins (*Copsychus sechellarum*) and is an important nesting area for lesser noddies (*Anous*

tenuirostris) with very high densities of these birds during the nesting season. This small habitat type needs to be conserved at all costs. It has been suggested, as a conservation measure, that *P. herculeaneus* could be translocated to other islands in their possible former range. Their presence and apparent thriving in *Pisonia* woodland lends itself to the establishment of translocated populations on islands with this type of habitat.

Habitat types 6 and 7 have changed from *Pterocarpus indicus* woodland as a result of sangdragon wilt which caused the die off of these trees by 2004. The beetles do not utilize the small trees in habitat number 6, yet utilize mature trees of the same species in habitat number 7. This indicates that these beetles prefer larger, mature trees and this is corroborated by Mellor (2002). In habitat number 6 they may be using decaying logs as habitat due to lack of larger trees. The high density of beetles in habitat number 7 indicates rapid dispersal into suitable habitat and shows the value of habitat restoration for this species. It is likely that these beetles will increase in numbers in habitat 6 over time, as the trees mature. The loss of *P. indicus* as a habitat type is not seen as being of any concern for the continued well being of the beetle. In contrast, it should be seen in a positive light as native species now replace what was an introduced species.

The absence of beetles in habitat number 15 is likely due to isolation and the inability to disperse as a result of adjacent coconut woodland. As is shown by the presence of beetles in mature restored habitat this habitat type should be of value to the beetle and the continued restoration of habitat on the island is strongly recommended, as long as it is carried out in a scientifically and ecologically sound manner. There is however concern that the use of *F. benghalensis* for restoration is detrimental not only to *P. herculeaneus* but for the general diversity of the island. It is strongly recommended that this practice be discontinued. Large areas of potential habitat are available for restoration work for the benefit of this and other species. Bamboo has been found to be of extremely low density and diversity for birds (Gane 2011) and spiders (Canning 2010) and is probably true of other species as well. This habitat is detrimental to biodiversity on the island and offers the possibility of substantially increasing available habitat should it be restored to native vegetation.

The method used to assess the population is not considered ideal as beetles present on the trees are likely to be missed. Those beetles that are high up the tree and sheltering out of sight, as well as those individuals that are on the top of branches are likely to be missed, giving an underestimation of the population. Weather conditions were also found to play a role in the abundance of beetles. In hot weather fewer beetles were visible, although surveying early in the morning nullified this problem. Heavy rain also reduces the abundance of visible beetles. The fact that these beetles are nocturnal (Ferguson & Pearce-Kelly 2004) may also bias the results of surveys carried out during the day, although their behaviour in the wild needs to be studied further to determine the best time for surveys. This method was chosen as it does lend itself to repeatability and allows for comparison of results from previous assessments. Regular monitoring of this species is needed to assess temporal population trends to ensure that continued vegetation and other changes do not negatively impact this species.

Although the population is stable and fairly significant, there is potentially far more habitat on the island available to support a larger population. With its' globally

restricted range and population size all efforts need to be taken to ensure the continued well being and expansion of the population. Fragmented habitats need to be connected to allow for dispersal and range expansion. The use of corridors is recommended where habitat types cannot be completely linked. These expanded areas of habitat will not only benefit this species, but other threatened species as well.

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